(US ISSN 0027-4100)

Bulletin OF THE
Museum of
Comparative
Zoology

Labroid Intrarelationships Revisited: Morphological Complexity, Key Innovations, and the Study of Comparative Diversity

MELANIE L. J. STIASSNY and JEFFREY S. JENSEN

HARVARD UNIVERSITY
CAMBRIDGE, MASSACHUSETTS, U.S.A.

VOLUME 151, NUMBER 5
22 APRIL 1987

(US ISSN 0027-4100)

PUBLICATIONS ISSUED OR DISTRIBUTED BY THE MUSEUM OF COMPARATIVE ZOOLOGY HARVARD UNIVERSITY

Breviora 1952–
Bulletin 1863–
Memoirs 1864–1938
Johnsonia, Department of Mollusks, 1941–
Occasional Papers on Mollusks, 1945–

SPECIAL PUBLICATIONS.

1. Whittington, H. B., and E. D. I. Rolfe (eds.), 1963. Phylogeny and Evolution of Crustacea. 192 pp.
2. Turner, R. D., 1966. A Survey and Illustrated Catalogue of the Teredinidae (Mollusca: Bivalvia). 265 pp.
3. Sprinkle, J., 1973. Morphology and Evolution of Blastozoan Echinoderms. 284 pp.
4. Eaton, R. J. E., 1974. A Flora of Concord. 236 pp.
5. Rhodin, G. J., and K. Miyata (eds.), 1983. Advances in Herpetology and Evolutionary Biology: Essays in Honor of Ernest E. Williams. 745 pp.

Other Publications.

Bigelow, H. B., and W. C. Schroeder, 1953. Fishes of the Gulf of Maine. Reprint.

Brues, C. T., A. L. Melander, and F. M. Carpenter, 1954. Classification of Insects.

Creighton, W. S., 1950. The Ants of North America. Reprint.

Lyman, C. P., and A. R. Dawe (eds.), 1960. Symposium on Natural Mammalian Hibernation.

Ornithological Gazetteers of the Neotropics (1975–).

Peters' Check-list of Birds of the World, vols. 1–15.

Proceedings of the New England Zoological Club 1899–1948. (Complete sets only.)

Publications of the Boston Society of Natural History.

Price list and catalog of MCZ publications may be obtained from Publications Office, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, 02138, U.S.A.

This publication has been printed on acid-free permanent paper stock.

LABROID INTRARELATIONSHIPS REVISITED: MORPHOLOGICAL COMPLEXITY, KEY INNOVATIONS, AND THE STUDY OF COMPARATIVE DIVERSITY

MELANIE L. J. STIASSNY and JEFFREY S. JENSEN[1]

ABSTRACT. The morphological and taxonomic implications of pharyngognathy in acanthomorph fishes are clarified, and the monophyly of the pharyngognath Labroidei is established. Characters bearing upon hypotheses of labroid intrarelationships are reviewed and a single minimum length tree is presented and discussed. Morphological character transformations within the Labroidei display a disconcertingly large amount of homoplasy and, until a single highly corroborated phylogeny is available, statements about relationships within the suborder must remain tentative.

The predominance of attributes of the pharynx and pharyngeal jaw apparatus as a major locus for character data in the diagnosis of the Labroidei is discussed, and the implications of pharyngeal dominance in systematic analyses are explored. Finally, we review the concept of the key innovation of labroid pharyngeal specialization as a causal explanation for the morphologic and taxonomic diversification of the Labroidei.

INTRODUCTION

The Labroidei, as conceived by Kaufman and Liem (1982), consists of the families Cichlidae, Embiotocidae, Labridae and Pomacentridae; together they include approximately 1,800 species (5–10% of all living fishes). The many ecological and evolutionary questions posed by the existence of species-rich, adaptively multiradiate, and often narrowly endemic communities of labroid fishes in tropical marine and freshwater biotopes occupy an important place in modern evolutionary studies (Futuyma, 1979; Greenwood, 1984; Stanley, 1979; Vrba, 1980; White, 1978). Systematists, ecologists, ethologists, geneticists, functional and evolutionary morphologists alike have probably focused on this group more than on any other neoteleostean clade. Within the last decade alone numerous publications have appeared dealing with questions of labroid development (Aerts, 1982; Claeys and Aerts, 1984; Morris and Gaudin, 1982), functional morphology (e.g., Dullemeijer, 1980; Dullemeijer and Barel, 1977; Gobalet, 1980; Liem, 1980, 1986; Liem and Sanderson, 1986; Strauss, 1984; Yamaoka, 1978, 1980), intrarelationships (e.g., Kaufman and Liem, 1982; Liem and Greenwood, 1981; Morris, 1982; Rosen, personal communication; Stiassny, 1980), ethology (e.g., Barlow and Munsey, 1976; Brett, 1979); and ecology (Hixon, 1980; Laur and Ebeling, 1983; Schmitt and Coyer, 1982; Witte, 1984).

Interest has also centered on the evolutionary dynamics of these fishes. To be open to scientific discussion and evaluation, however, hypotheses concerning the operation of evolutionary processes such as modes and rates of speciation, the acquisition and role of evolutionary novelties, and niche-space utilization need a corroborated and precise theory of phylogenetic interrelationships (Eldredge and Cracraft, 1980; Lauder, 1981, 1982a; Nelson and Platnick, 1981; Wiley, 1981). The concept of a coherent labroid assemblage has only recently emerged (e.g., Kaufman and Liem, 1982; Liem and Greenwood, 1981), and we are still far from a consen-

[1] Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138.

sus regarding the intrarelationships of this important clade.

Since the families comprising the Labroidei were originally united as the Acanthopterygii Pharyngognathy in the predarwinian classification of Müller (1843), attributes of the pharynx and pharyngeal jaw apparatus have played a singularly important role in labroid systematics. Our study further establishes the predominance of the pharyngeal jaw apparatus as the major locus for character data in the systematic diagnosis of the Labroidei and explores its possible implications in systematic analyses.

Recent research suggests that features of the pharynx, and in particular the labroid pharynx, have important evolutionary consequences not only for systematic studies, but for the diversification of the clade as well (e.g., Liem, 1973, 1980; Liem and Sanderson, 1986). It has long been speculated that intrinsic features of design can play a major role in evolution (Lauder, 1982b; Russell, 1982), and the key innovation of labroid pharyngeal specialization is a much cited explanatory case. We review the concept of the key innovation as a causal explanation for the morphological and taxonomic diversification of the Labroidei.

MATERIALS

Specimens were dissected under a Wild M-7 stereomicroscope, and drawings made with the aid of a camera lucida attachment. Osteological specimens were cleared and double stained following the procedure of Dingerkus and Uhler (1977). A complete list of materials including catalogue numbers is available from the senior author on request. Nomenclature of the muscles follows that of Winterbottom (1974) and Anker (1978). Topographical and skeletal nomenclature is based upon that of Nelson (1969), Rosen (1973) and Barel *et al.* (1976).

The following specimens were studied. Abbreviations in parentheses following species names refer to condition of specimens examined: c.s. (=cleared and double stained) skel. (=skeleton) and alc. (=alcohol preserved).

Labroidei

Cichlidae: *Acaronia nassa* (c.s., alc.), *"Aequidens" coeruleopunctatus* (c.s., alc.), *"Ae." potaroensis* (alc.), *Astatotilapia bloyeti* (c.s., alc.), *Astronotus ocellatus* (skel.), *Cichla ocellaris* (c.s., alc.), *Cichlasoma bimaculatum* (c.s., alc.), *C. (Heros) severum* (c.s.), *Crenicichla alta* (c.s., alc.), *Ctenochromis horii* (c.s., alc.), *Etroplus suratensis* (c.s., alc.), *Geophagus surinamensis* (c.s., alc.), *Hemichromis bimaculatus* (c.s., alc.), *Oreochromis mossambicus* (c.s., alc.), *Orthochromis malagarensis* (c.s.), *Paratilapia polleni* (c.s., alc.), *Pelmatochromis buettikoferi* (c.s.), *Sarotherodon galilaeus* (c.s., alc.), *Tylochromis jentinki* (c.s., alc.)

Labridae: *Bodianus diplotaenia* (alc.), *B. rufus* (c.s.), *Coris julis* (alc.), *Crenilabrus melops* (c.s., alc.), *Halichoeres poeyi* (c.s.), *Labrichthys unilineatus* (c.s., alc.), *Labroides dimidiatus* (c.s., alc.), *Labrus bergylta* (c.s., alc.), *Lachnolaimus maximus* (skel.), *Pseudojulis notospilus* (c.s.), *Scarus* sp. (c.s.), *Sparisoma* spp. (c.s.), *Symphodus rostratus* (c.s.), *Tautoga onitis* (skel.), *Tautogolabrus adspersus* (c.s., alc.), *Thalassoma bifasciatum* (c.s.)

Embiotocidae: *Cymatogaster aggregata* (c.s., alc.), *Damalichthys vacca* (c.s., alc.), *Ditrema temmincki* (c.s., alc.), *Embiotoca lateralis* (c.s., alc.), *Hyperprosopon argenteum* (c.s.), *Hysterocarpus traski* (c.s.), *Micrometrus minimus* (c.s.), *Neoditrema ransonnetti* (c.s.), *Phanerodon furcatus* (c.s., alc.), *Zalembius rosaceus* (c.s.)

Pomacentridae: *Abudefduf troschelli* (c.s., alc.), *A. saxatilis* (c.s., alc.), *Amphiprion allardi* (c.s., alc.), *Chromis atrilobata* (c.s., alc.), *C. cyaneus* (c.s., alc.), *Dascyllus albisella* (alc.), *Eupomacentrus planifer* (c.s.), *Microspathodon chrysurus* (alc.), *Neopomacentrus sindensis* (c.s., alc.), *Nexilaris taurus* (alc.), *Pomacentrus otophorus* (c.s., alc.), *P. moluccensis* (c.s.,

alc.), *Pristotis jerdoni* (c.s.), *Stegastes acapulcoensis* (c.s., alc.), *S. fuscus* (c.s., alc.)

Percomorph Outgroups

"Basal" Percoids

Centrarchidae: *Centrarchus macropterus* (c.s.), *Lepomis macrochirus* (c.s., alc.), *Micropterus dolomieui* (c.s., alc.), *M. salmoides* (alc.), *Pomoxis* sp. (c.s.)

Centropomidae: *Centropomus pectinatus* (c.s., alc.), *Lates niloticus* (c.s.)

Lutjanidae: *Lutjanus blackfordi* (skel.), *Lutjanus synagris* (c.s., alc.), *Rhomboplites aurorubens* (skel.)

Percidae: *Perca flavescens* (c.s., alc.), *Etheostoma olmstedi* (c.s., alc.)

Perchichthyidae: *Morone americana* (c.s.), *M. saxatilis* (c.s., alc.), *Perchichthys trucha* (c.s., alc.)

Serranidae: *Diplectrum radiale* (alc.), *Epinephelus striatus* (alc.), *Serranus cabrilla* (c.s., alc.), *S. fasciatus* (c.s., alc.), *S. hepatus* (c.s., alc.), *Synagrops bellus* (c.s., alc.)

Percoid Taxa "Close" to the Labroidei

Gerreidae: *Eucinostomus gula* (c.s., alc.), *Gerres cinereus* (alc.), *G. filamentosus* (c.s.), *G. poieti* (c.s.)

Haemulonidae: *Anisotremus virginicus* (skel.), *Anisotremus* sp. (c.s.), *Haemulon album* (alc.), *H. flavolineatum* (c.s., alc.), *Pomadasys crocro* (c.s., alc.)

Kyphosidae: *Kyphosus* spp. (c.s., alc.)

Lethrinidae: *Lethrinus* spp. (c.s., alc.)

Sparidae: *Boops boops* (c.s., alc.), *Crenidens crenidens* (c.s.), *Diplodus vulgaris* (c.s., alc.), *Pagellus erythrinus* (c.s., alc.)

Scorpididae: *Scorpis chilensis* (alc.), *Scorpis* sp. (c.s., alc.)

Additional Percoid Outgroups

Apogonidae: *Apogon maculatus* (c.s.), *Cheilodipterus macrodon* (c.s.)

Bramidae: *Brama dussumieri* (c.s.)

Carangidae: *Caranx crysos* (c.s.), *Decapterus macarellus* (c.s., alc.) *Trachinotus* sp. (skel.)

Cepolidae: *Cepola rubescens* (c.s., alc.)

Chaetodontidae: *Chaetodon* spp. (skel.)

Pomacanthidae: *Pomacanthus paru* (skel.)

Cirrhitidae: *Cirrhitichthys maculatus* (skel.)

Girellidae: *Girella albostriata* (c.s., alc.)

Leiognathidae: *Leiognathus klunzingeri* (c.s., alc.), *Leiognathus* sp. (c.s.)

Mastacembelidae: *Mastacembelus brachyrhinus* (c.s.)

Mullidae: *Mulloidichthys martinicus* (c.s.), *Upneus maculatus* (c.s., alc.)

Mugilidae: *Agonostomus monticola* (c.s., alc.), *Mugil curema* (c.s., alc.)

Pempheridae: *Pempheris* sp. (c.s.)

Pomatomidae: *Pomatomus saltatrix* (c.s., alc.)

Sciaenidae: *Pogonias cromis* (c.s., alc.), *Menticirrhus americanus* (c.s.), *Otolithes ruber* (c.s., alc.), *Pseudosciaena axillaris* (c.s.)

Anabantoidei

Anabantidae: *Anabas testudineus* (c.s., alc.), *Ctenopoma multispinis* (c.s., alc.), *Sandelia capensis* (c.s.)

Belontiidae: *Betta pugnax* (c.s., alc.)

Blennioidei

Blenniidae: *Blennius gattorgine* (skel.)

Pholidae: *Aplodichthys flavidus* (skel.)

Gobioidei

Eleotrididae: *Gobiomorus dormitor* (c.s., alc.)

Gobiidae: *Bathygobius soporator* (skel., c.s.), *Gillichthys mirabilis* (skel.) *Gobius niger* (skel.)

Acanthuroidei

Acanthuridae: *Acanthus chirurgus* (skel.), *A. triostegus* (skel.)

Siganidae: *Siganus* sp. (c.s.)

Balistoidei

Balistidae: *Balistes* sp. (skel.), *Melichthys ringens* (skel.)

Tetraodontidae: *Tetradon* sp. (skel.)
Diodontidae: *Diodon hystrix* (skel.)

Cyprinodontoidei

Cyprinodontidae: *Orestias cuvieri* (c.s.), *O. ispi* (c.s.)
Fundulidae: *Fundulus diaphanus* (c.s., alc.)
Atherinidae: *Atherinops* sp. (c.s.), *Menidia menidia* (c.s., alc.)

Exocoetoidei

Exocoetidae: *Exocoetus obtusirostris* (alc.), *E. volitans* (alc.), *Cypselurus cyanopterus* (skel.), *Parexocoetus brachypterus* (c.s., alc.)
Hemiramphidae: *Euleptorhamphus velox* (alc.), *Hemiramphus balao* (alc.), *H. brasiliensis* (skel.), *Hemiramphus* sp. (skel.), *Hemirhamphodon* sp. (alc.), *Oxyporhamphus micropterus similis* (alc.), *Hyporhamphus sajori* (alc.)
Belonidae: *Ablennes hians* (alc.), *Belone belone* (alc.), *Belone* sp. (skel.), *Platybelone argalus* (alc.), *Strongylura timucu* (alc.), *Tylosurus acus acus* (alc.), *T. crocodilus* (alc.)
Scomberesocidae: *Scomberesox saurus* (alc.), *Scomberesox* sp. (c.s., alc.), *Nanichthys simulans* (alc.)

METHODS

The size and intrafamilial diversity of labroid lineages, in combination with a lack of precise knowledge of intralineal relationships, makes selection of appropriate representatives problematical. For this reason, after an initial anatomical review within each major clade, we attempted to select a single taxon to represent the plesiomorphic familial condition for each of the characters or character complexes under investigation. Clearly it is not always the same taxon that bears the plesiomorphous state for each character under consideration (see also Stiassny, 1986). In addition to the data derived from the present review, a suite of characters relevant to the resolution of labroid monophyly and intrarelationships was compiled from a comprehensive literature survey. For characters that have previously appeared in the literature we offer a reassessment of their value as indicators of phylogenetic relationship along with a citation of pertinent literature. Although all of the characters cited in previous analyses, as well as those novel to this study, are considered in the Character Survey section, we have been selective in those that we entered into the final analysis of labroid intrarelationships. Typically, a character was excluded from analysis for one of the following reasons:

1) We disagree with previous homology assessments; 2) The character distribution is highly variable and/or uninformative; 3) In one case, the distribution among outgroups is so variable as to render polarity determination highly problematical. Although several characters are excluded from our analysis, we include a discussion of these characters and make explicit our rationale for exclusion in each case. For ease of critical review we have included our data matrix in Appendix 1.

Throughout the study character polarity was assessed by the Outgroup Method (Maddison *et al.*, 1984; Stevens, 1980; Watrous and Wheeler, 1981). In the absence of a well worked-out scheme of labroid interrelationships, selection of appropriate outgroup taxa poses a problem. In view of the importance of outgroup designation in an analysis of this kind we have attempted to mitigate the situation by reviewing a wide range of percomorph taxa and selecting two groups of outgroup taxa for particular attention. The first group included representatives of some of the families thought to be "primitive" or "basal" perciforms (Gosline, 1966; Johnson, 1980, 1984; Regan, 1913; Stiassny, 1981). The second group included representatives of those families that have been suggested by previous authors to be "close" to the Labroidei. This group included members of the Sparidae and Gerreidae (Stiassny, 1980, 1981), Kyphosidae (Tarp,

1952), Scorpididae (Morris, 1982), Haemulonidae and Lethrinidae (Rosen, personal communication). In addition, we examined a further range of percomorph taxa including a number of other pharyngognathous acanthomorphs. Where possible, outgroup families are represented by the most morphologically generalized of their genera available to us.

A minimum length tree for the included data was derived using the branch and bound algorithm of PAUP version 2.4 (Phylogenetic Analysis Using Parsimony, Swofford, 1985) with Farris (1972) optimization. The tree was rooted by designating a hypothetical taxon representing an outgroup possessing the presumed primitive state for all characters included. All characters were coded as two state characters (see Appendix 1) of equal weight. In addition to computing the shortest tree, alternative topologies, of which 14 are possible, were also explored using PAUP (Swofford, 1985) and MacClade version 1.0 (Maddison, 1986). For the purposes of our analysis we assumed familial monophyly for each of the component labroid families (Kaufman and Liem, 1982; Stiassny, 1980), and made no concerted effort to consistently sample the range of potential autapomorphies available for analysis. However, where a novel autapomorphy was identified we noted its presence and justified our assessment of its status. As the monophyly of the four major labroid lineages has been established previously (e.g., Kaufman and Liem, 1982), characters autapomorphic for the component taxa were not included in the intra-subordinal analysis.

LABROID MONOPHYLY AND THE CONCEPT OF PHARYNGOGNATHY

Despite a considerable amount of recent attention there remains much confusion about the morphological and taxonomic implications of what has been termed pharyngognathy in acanthomorph fishes (Kaufman and Liem, 1982; Liem and Greenwood, 1981; Morris, 1982; Rosen, personal communication). A clarification of the concept, in particular as it has been applied to labroids, provides a helpful introduction to our investigation of labroid monophyly and intrarelationships.

The complex series of modifications of the pharyngeal jaw apparatus (PJA) resulting in the emergence of the mobile upper and lower pharyngeal jaws of euteleostean fishes has been well documented (Lauder, 1983; Nelson, 1967b, 1969; Rosen, 1973). Once that euteleostean level of organization was attained, the basic components were then available for subsequent modification along an impressive array of difference lines. Within the Acanthomorpha, perhaps in reflection of the high degree of pharyngeal modification exhibited by that clade, characteristics of the PJA have played an increasingly central role in attempts to elucidate phylogenetic interrelationships (e.g., Rosen, 1973, 1985; Rosen and Parenti, 1981).

Pharyngognathy, as originally conceived, is the possession of united fifth ceratobranchials. Gunther (1880), following Müller (1843), used pharyngeal morphology to characterize the order Acanthopterygii Pharyngognathii which he defined in part by the shared possession of "lower pharyngeal bones coalesced into a single unit." Numerous authors have questioned Gunther's interpretation of phyletic integrity, which included in the group pomacentrids, labrids, embiotocids, and cichlids (=chromides of Gunther, 1880), and many have proposed alternative classifications for these taxa (e.g., Berg, 1940; Bertin and Arambourg, 1958; Greenwood *et al.*, 1966; Jordan, 1905; Norman, 1966; Regan, 1913).

More recently, however, in a series of papers using a range of different approaches, Liem and his coworkers address the problems of pharyngognathy, labroid monophyly and interrelationships (Kaufman and Liem, 1982; Lauder and Liem, 1983; Liem, 1973, 1986; Liem and Greenwood, 1981; Liem and Osse, 1975; Liem and Sanderson, 1986). One result of this

work is the growing consensus that Müller's original grouping has phyletic integrity, a notion formalized by Kaufman and Liem (1982) with the assembly of these taxa into the Suborder Labroidei.

The Labroidei of Kaufman and Liem (1982) is defined on the basis of three pharyngeal characters: 1) Junction or fusion of the two fifth ceratobranchial bones into a single unit; 2) Diarthrosis (bone to bone contact) between upper pharyngeal jaws and the basicranium; 3) Presence of the sphincter oesophagi muscle as a continuous sheet, with no dorsal subdivision.

A review of these and other pharyngeal features enables us to refine the concept of labroid monophyly, and the use of the term pharyngognathy in morphological studies. Throughout this section summary statements of characters assessed to be synapomorphic for the Labroidei are italicized.

Among acanthomorphs there exists an array of diverse lineages each with representatives in which the pharyngeal jaws are hypertrophied (relative to non-pharyngognathous members of their respective clades), and the fifth ceratobranchials comprising the LPJ are united into a single functional unit. In addition to the labroids, Liem and Greenwood (1981) and Kaufman and Liem (1982) cited members of the Anabantidae (Figs. 1E, F), Kyphosidae, Pomadasyidae, Centrarchidae, Carangidae, Sciaenidae (Fig. 1A) and Cyprinodontoidei (see also Parenti, 1984) as bearing fused or otherwise joined lower pharyngeal jaws. Actually this list should be extended to include (some but not all) members of the Gerreidae (Fig. 1C), Leiognathidae (Fig. 1D), Sparidae and Haemulonidae (Rosen, ms), Pholidichthyidae (Springer and Freihofer, 1976), Lutjanidae (Johnson, 1980) and members of the Beloniformes[2] (Figs. 2B, C).

Comparison of the pharyngeal jaws in a range of percomorph taxa illustrates that the nature of the LPJ union differs markedly within the assemblage. In the majority of percoids with a hypertrophied pharynx the LPJ is formed by the close apposition of the two fifth ceratobranchials. The union is mediated by a simple straight suture reinforced ventrally by a concentration of connective tissue. This is also the case in the anabantoids examined (Figs. 1E, F). In pharyngognath gerreids (Fig. 1C) and sciaenids (Fig. 1A), as well as in virtually all cichlids (the single exception being the autapomorphic condition in *Cichla*, discussed by Stiassny, 1982 and in press), the suture is convoluted caudally and the contralateral elements interdigitate (e.g., Fig. 3B). Among cyprinodonts both the straight suture and the interdigitating type are expressed (see figures in Rosen, 1964; Rosen and Parenti, 1981). Finally, in the non-cichlid labroids (Figs. 3A, C, D), as well as in exocoetoid beloniforms (Figs. 2B, C), there is a complete fusion of the two LPJ elements and no trace of a central sutural union is evident. The phylogenetic implications of these different modes of union within the Acanthomorpha is unclear, although in the Labroidei the condition of complete fusion is interpreted as a synapomorphy of labrids, pomacentrids and embiotocids (page 288).

In view of the mosaic distribution of this character, the presence of coalesced lower pharyngeal jaws as a defining character of labroids is, by itself, rather weak (but see page 286 for further discussion). Indeed the "tendency" towards the expression of pharyngognathy (co-occuring with hypertrophy of the PJA) would appear to be extremely widespread

[2] Due to a lack of material available for examination, we have not included members of the family Adrianichthyidae in our analysis. Details of pharyngeal morphology of these fishes are few, but some data are presented in Rosen (1964) and Rosen and Parenti (1981). The adrianichthyoids are notable among beloniforms in lacking a united and medially fused LPJ. Throughout this paper we adopted Rosen and Parenti's (1981) classification of the Beloniformes (Fig. 7; see also Collette *et al.*, 1984).

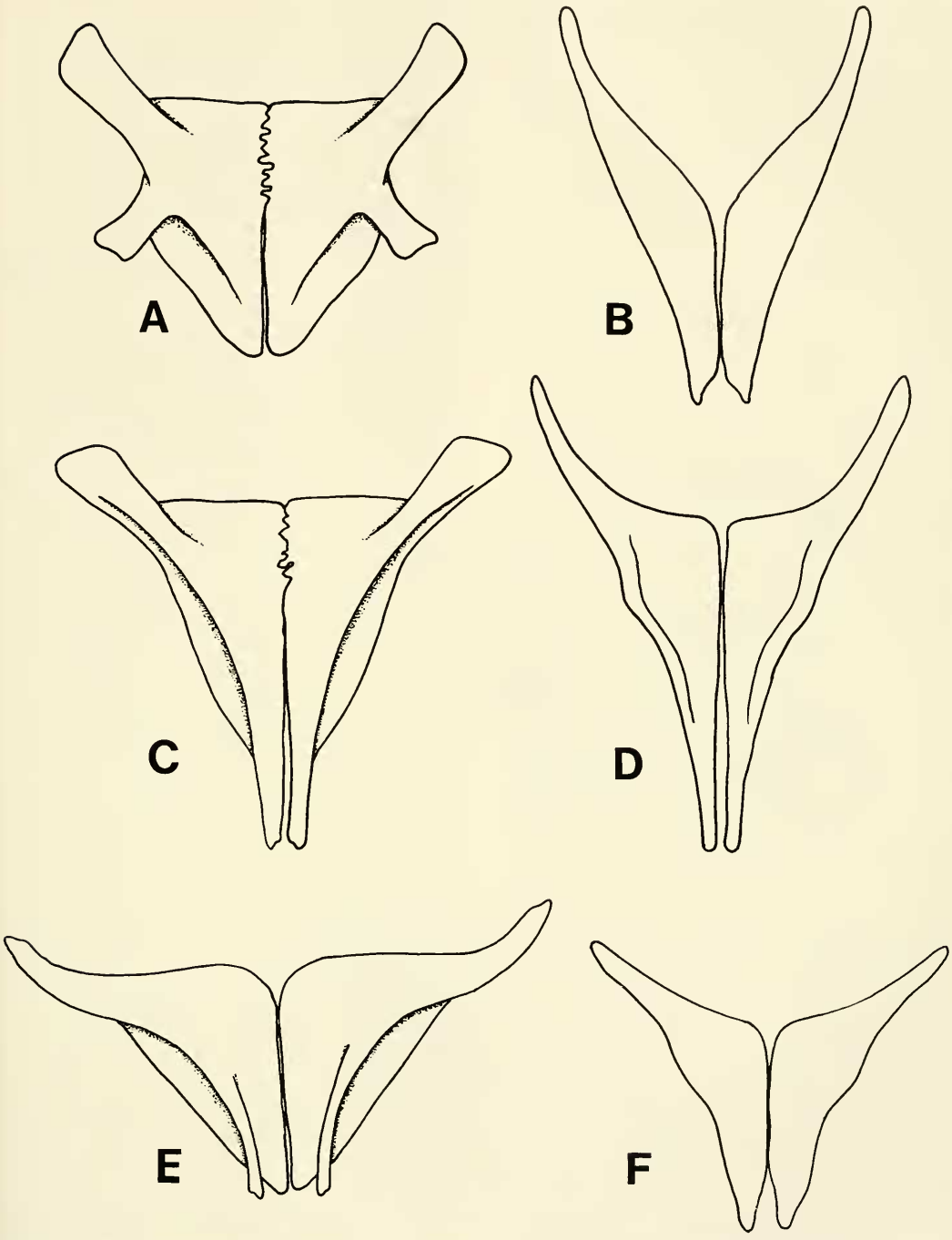


Figure 1. Lower pharyngeal jaw in ventral view. A. *Pogonias*; B. *Menticirrhus*; C. *Gerres*; D. *Leiognathus*; E. *Anabas*; F. *Sandelia*.

Abbreviations for this and the following figures are listed at the end of the text under Appendix 2.

among percomorphs, as well as in Rosen and Parenti's (1981) division II of the Atherinomorpha.

One feature of the LPJ appears to be unique (among perciforms) to the labroids and as such strengthens the claim of labroid monophyly. In all labroid taxa the LPJ bears a well-developed median keel on the ventral face of the bone (Fig. 3A–D). This blade-like keel serves as an attachment site for a part (or all, in some labrids and cichlids) of the transversus ventralis muscle (Fig. 4). Primitively among acanthomorphs the transversus ventralis is bipartite (TV V and IV), the second of these muscles (IV) passes from the fourth ceratobranchial of one side to insert on the contralateral element, thus entirely bypassing the fifth ceratobranchials (e.g., Fig. 4A). Although in a few other so-called higher percoid lineages the transversus ventralis is reduced to a single muscle (IV), in these taxa it passes between fourth ceratobranchials and has no insertion onto the LPJ keel. *The presence of a blade-like keel on the LPJ and the presumably correlated shift in insertion of part (or all) of the transversus ventralis onto that keel constitutes a synapomorphy of the Labroidei.*

In exocoetoid beloniforms a remarkably similar arrangement of pharyngeal keel and transversus ventralis insertion is present.

Primitively among perciforms the transversus dorsalis anterior muscle is bipartite and, following the nomenclature of Anker (1978), the two components are designated the m. cranio-pharyngobranchialis 2 and the m. transversus epibranchialis 2 (e.g., Figs. 5C, D). Within the Labroidei the percomorph muscle configuration has undergone a partial reduction and the *pomacentrids, embiotocids and labrids are characterized by the lack of the anterior muscle component, i.e., the m. cranio-pharyngobranchialis 2* (see Stiassny, 1980 figs. 22, 23, 24; Kaufman and Liem, 1982 fig. 2). A well-developed m. cranio-pharyngobranchialis 2 is present in all cichlid taxa (e.g., Fig. 6E). An elaboration of the percomorph configuration of the transversus dorsalis is also evident among labroids and in cichlids (Fig. 6E), pomacentrids and labrids (Kaufman and Liem, 1982; Stiassny, 1980) a third division of the muscle is developed (the m. transversus pharyngobranchialis 2; Fig. 6E). Uniquely among acanthomorphs, the embiotocid transversus dorsalis anterior muscle complex is represented by a single component (the m. transversus epibranchialis 2). The embiotocid condition could have been derived by a reduction from the primitive bipartite percomorph condition or it could represent a reduction from the tripartite state of the remaining Labroidei. Although not strictly the most parsimonious interpretation, Stiassny (1980) adopted the second alternative. She regarded the presence of a m. transversus pharyngobranchialis 2 muscle division to be synapomorphic for labroids and interpreted the absence of the division in embiotocids as a secondary loss reflecting an extension of the reductive trend already noted in the loss of the cranio-pharyngobranchialis 2 of embiotocids, labrids and pomacentrids. Following the same reasoning, and with due reservation, we concur with Stiassny (1980) in her interpretation and assess *the presence of a m. transversus pharyngobranchialis 2 division of the transversus dorsalis anterior muscle to be a synapomorphy of the Labroidei (secondarily reduced in the Embiotocidae).* However, the alternative interpretation of a cichlid/labrid/pomacentrid alignment based upon transversus elaboration is clearly posed.

According to Liem and Greenwood (1981) the Cichlidae are characterized by an additional subdivision of the m. transversus epibranchialis 2 (see Anker, 1978), resulting in a quadripartite transversus anterior muscle. The Labridae also bears a quadripartite transversus dorsalis anterior complex, but in these fishes the additional muscle part is a m. transversus epibranchialis (Stiassny, 1980). Reduction

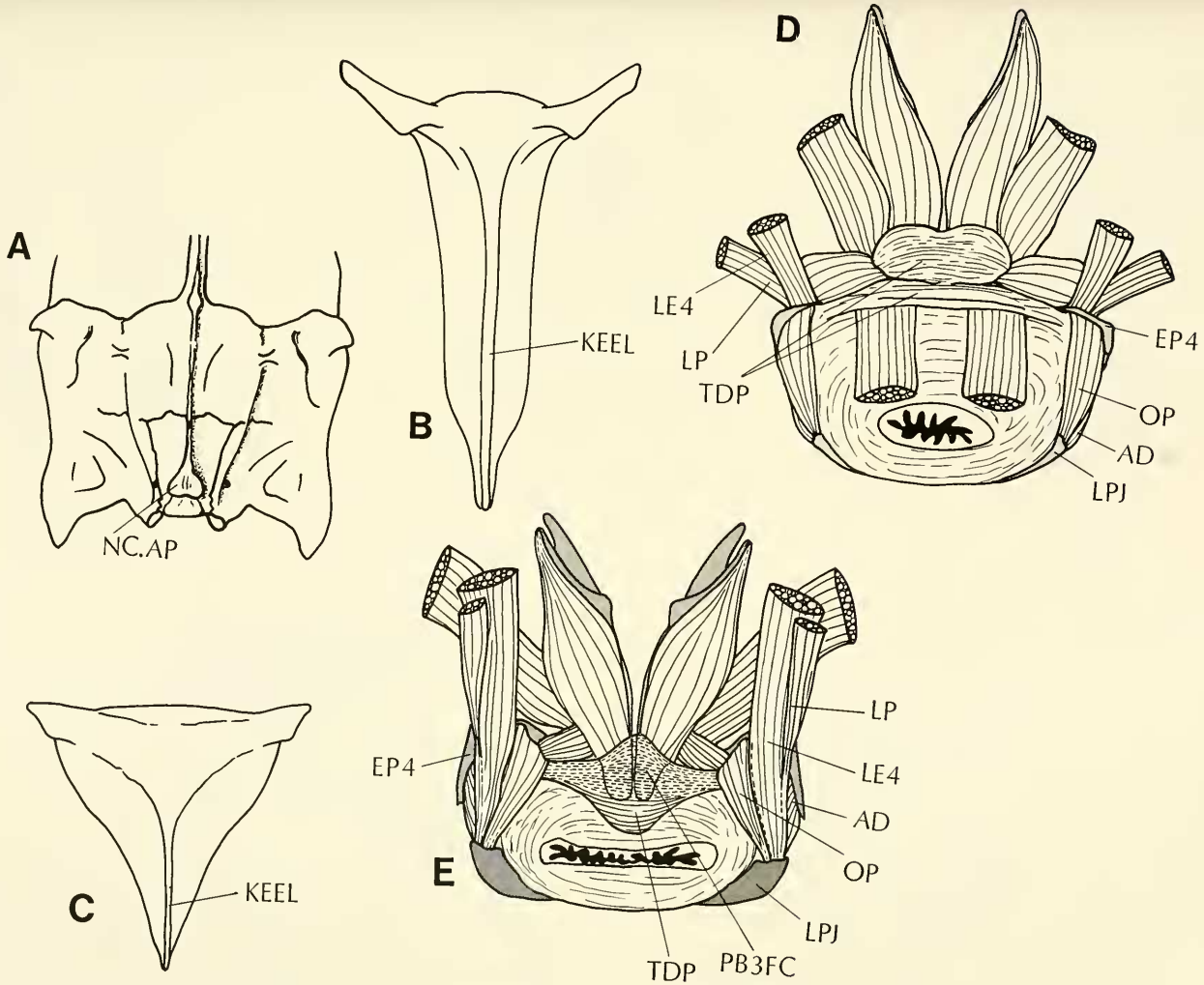


Figure 2. Aspects of the beloniform pharyngeal jaw apparatus. A. *Exocoetus* pharyngeal apophysis (ventral view); B. *Belone* LPJ (ventral view); C. *Exocoetus* LPJ (ventral view); D. *Strongylura* isolated PJA (dorsal view); E. *Exocoetus* isolated PJA (dorsal view).

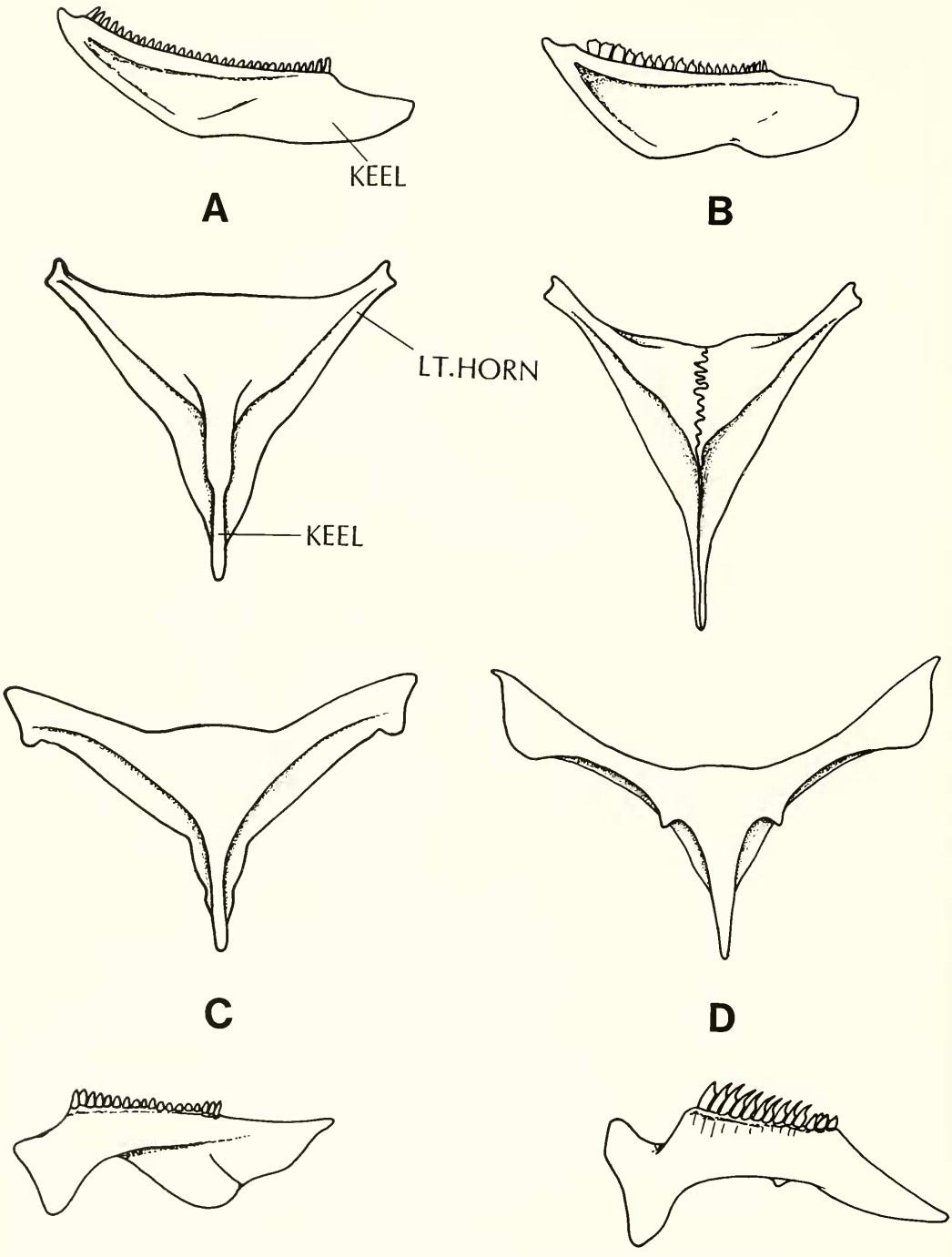


Figure 3. Lower pharyngeal jaw in lateral and ventral view. A. *Embiotoca*; B. *Astatotilapia*; C. *Labrus*; D. *Pomacentrus*.

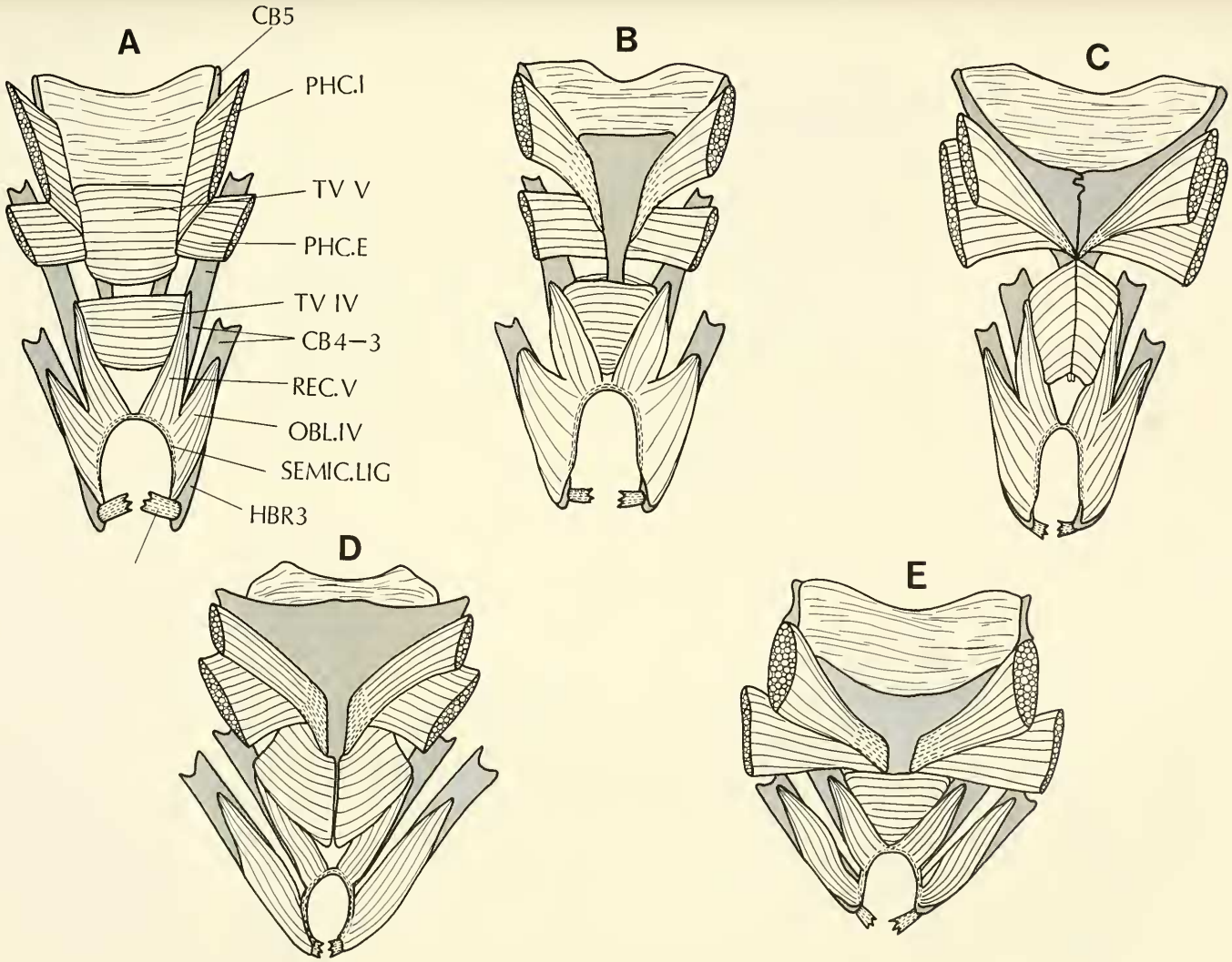


Figure 4. Ventral branchial arch musculature of: A. *Morone*; B. *Embiotoca*; C. *Astatotilapia*; D. *Labrus*; E. *Pomacentrus*, in ventral view.

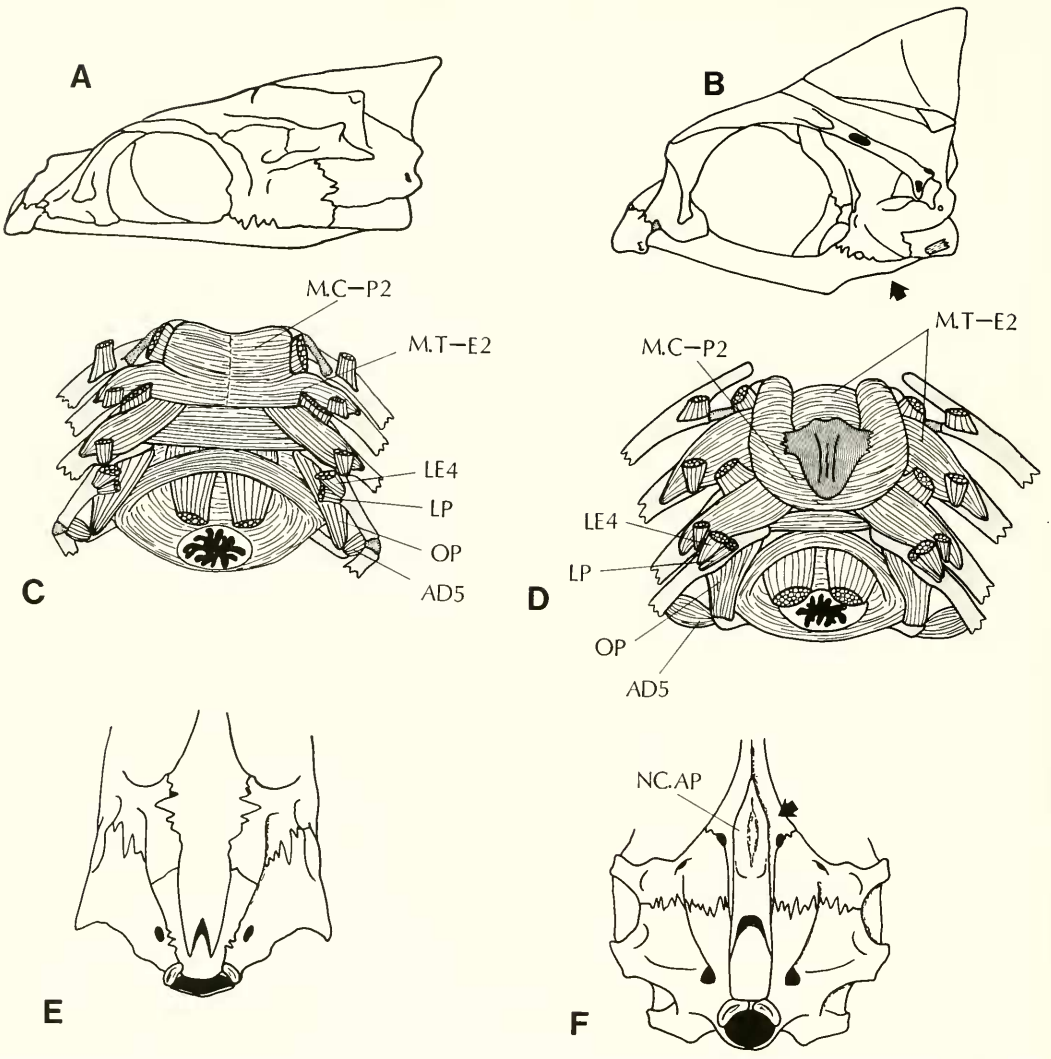


Figure 5. Aspects of the percoid pharyngeal jaw apparatus. A. *Morone* neurocranium (lateral view); B. *Diplodus* neurocranium (lateral view); C. *Morone* isolated PJA (dorsal view); D. *Diplodus* isolated PJA (dorsal view); E. *Morone* postorbital region of the neurocranium (ventral view); F. *Diplodus* pharyngeal apophysis (ventral view).

of the transversus dorsalis anterior to a single component—the m. transversus epibranchialis 2—is a synapomorphic feature of embiotocids.

Kaufman and Liem's (1982) second character, the presence in labroids of a true diarthrosis between upper pharyngeal jaws and the basicranium has been discussed by Stiassny (1980, 1982), however some additional clarification is helpful here.

In labroids the transversus dorsalis anterior and the transversus dorsalis posterior muscles do not completely overlie the raised articular facets borne on the third pharyngobranchials of the upper pharyngeal jaws (UPJ), and these bony facets are exposed (e.g., Fig. 6E; see also

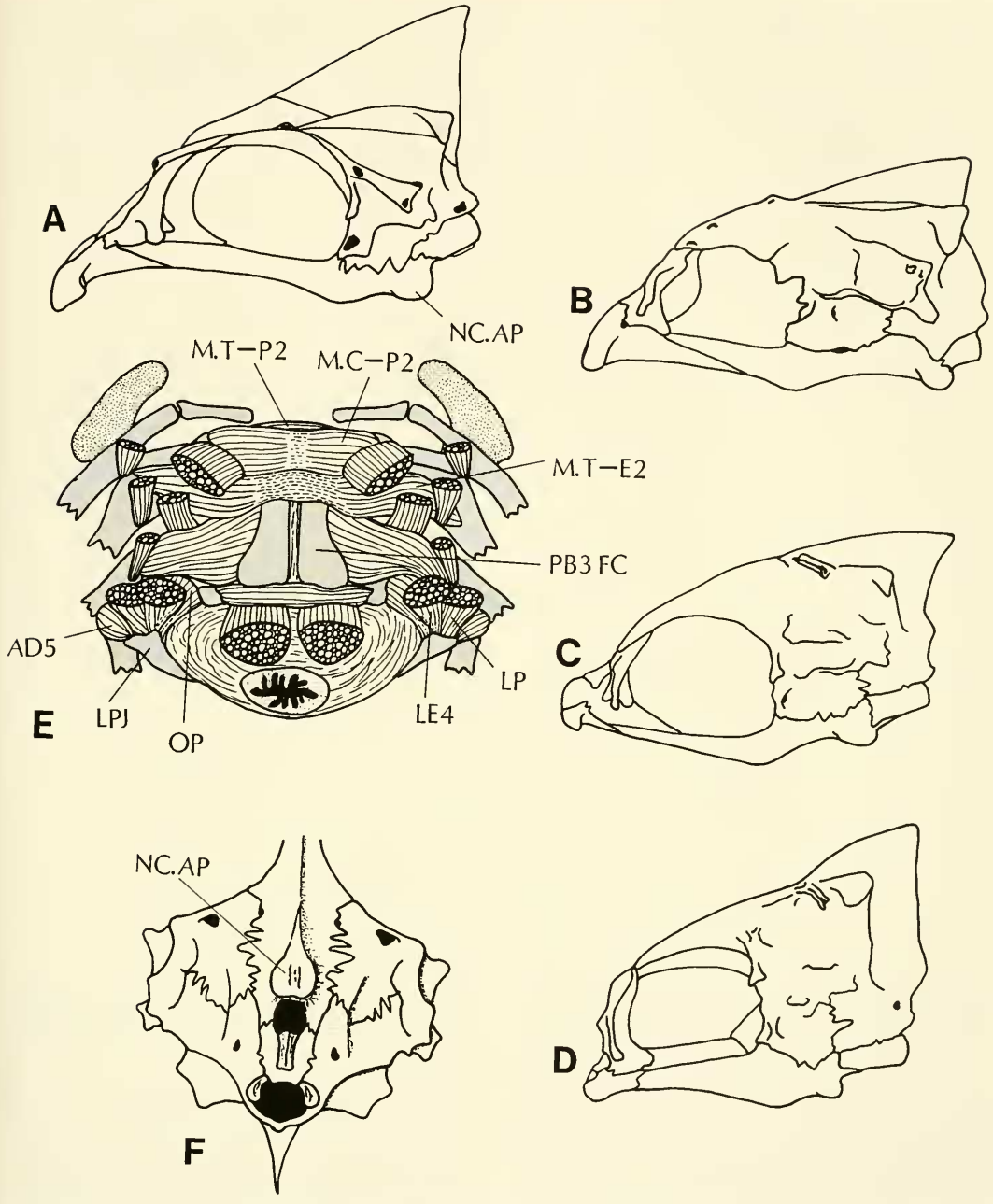


Figure 6. Aspects of the labroid pharyngeal jaw apparatus. A. *Tylochromis* neurocranium (lateral view); B. *Labrus* neurocranium (lateral view); C. *Embiotoca* neurocranium (lateral view); D. *Pomacentrus* neurocranium (lateral view); E. *Tylochromis* isolated PJA (dorsal view); F. *Tylochromis* pharyngeal apophysis (ventral view).

figures in Kaufman and Liem, 1982; Liem and Greenwood, 1981). On the skull base the LPJ facets are opposed by a raised neurocranial apophysis (Figs. 6A–D; see also Greenwood, 1978). This is not the case in "lower percoids" (e.g., *Serranus* Stiassny, 1982; *Morone*, Fig. 5C) where the entire dorsal face of the UPJ is covered by muscle and the skull base bears no articulatory or apophyseal structure (Fig. 5E). In pharyngognath members of the Gerreidae, Leiognathidae, Sciaenidae, Sparidae (e.g., Figs. 5B, D, F), and Girellidae a quite different situation pertains. In these taxa the transversus dorsalis anterior muscle complex is hypertrophied, and the cranio-pharyngobranchialis 2 forms a muscular "cushion" over the UPJ; the median connective tissue raphe, which is merely a longitudinal septum in *Morone* (Fig. 5C), is hypertrophied forming a substantial fibrous pad that overlies the muscle and is sculptured to fit closely into a grooved apophysis borne on the skull base (Figs. 5D, F). Although there is considerable variation in the form of the corresponding neurocranial apophyses, ranging from the strongly indented cup-like parasphenoid structure of *Pogonias* to the ventral thickening and reinforcement of the paraphenoid in *Diplodus* (Fig. 5F), in none of these taxa does the apophysis have the same morphology as that of labroids.

Based on these observations we consider the form of the labroid neurocranial apophysis highly characteristic of that clade. In labroids the articular surface is borne on a ventrally projecting apophysis formed in most cases by the parasphenoid and supported dorsally by the ventral margin of the prootic of each side. In some cichlids and embiotocids the basioccipitals also contribute to the articular surface of the apophysis (see Greenwood, 1978; Morris, 1982). In lateral view the apophysis of labroid fishes can clearly be seen as a rounded ventral projection (NC.AP in Figs. 6A–D). Greenwood (1978: 301) noted that the apophysis of certain labrids is structurally very similar to that of certain cichlids, but concluded that ". . . the gross morphology is quite unlike that in the cichlids." While we agree that the labrid apophysis is highly characteristic of that clade (see e.g., figs. in Rognes, 1973) we disagree that it is "quite unlike" that of other labroids. Thus, although a neurocranial apophysis of some form is commonly developed in other pharyngognath acanthomorphs, in no case is the apophysis developed in the same way or to the same extent as that described and illustrated here for the labroids. We propose that, in addition to sharing the synapomorphy of the presence of a true diarthrosis (bone to bone contact) between the neurocranial base and the third pharyngobranchials, *the labroids are further characterized by the synapomorphic presence of a ventrally projecting rounded form of the neurocranial apophysis.*

An interesting parallel is also found among beloniform fishes. In exocoetids (Exocoetidae and Hemiramphidae) a well-developed neurocranial apophysis (but formed entirely by the basioccipital bone) articulates with exposed dorsal facets on the third pharyngobranchials (Fig. 2A). The exposure of the third pharyngobranchials is brought about by a modification of the anterior portion of the transversus dorsalis posterior muscle into a thin connective tissue sheet (Fig. 2E). Contrasted with this is the condition of the complex in scomberesocids (Belonidae and Scomberesocidae) where, although a well-developed basioccipital apophysis is present on the neurocranium, articulation with the pharyngobranchial facets is interrupted by a thickened region of connective tissue of the transversus dorsalis muscle, as well as by the muscle itself (Fig. 2D).

The sphincter oesophagi muscle is subdivided in all of the nonlabroid percomorph taxa examined during the course of this investigation, and the lack of the subdivision is confirmed as being a synapomorphy of the Labroidei (Stiassny, 1980). The dorsal division of the sphincter oesophagi is greatly reduced (scombere-

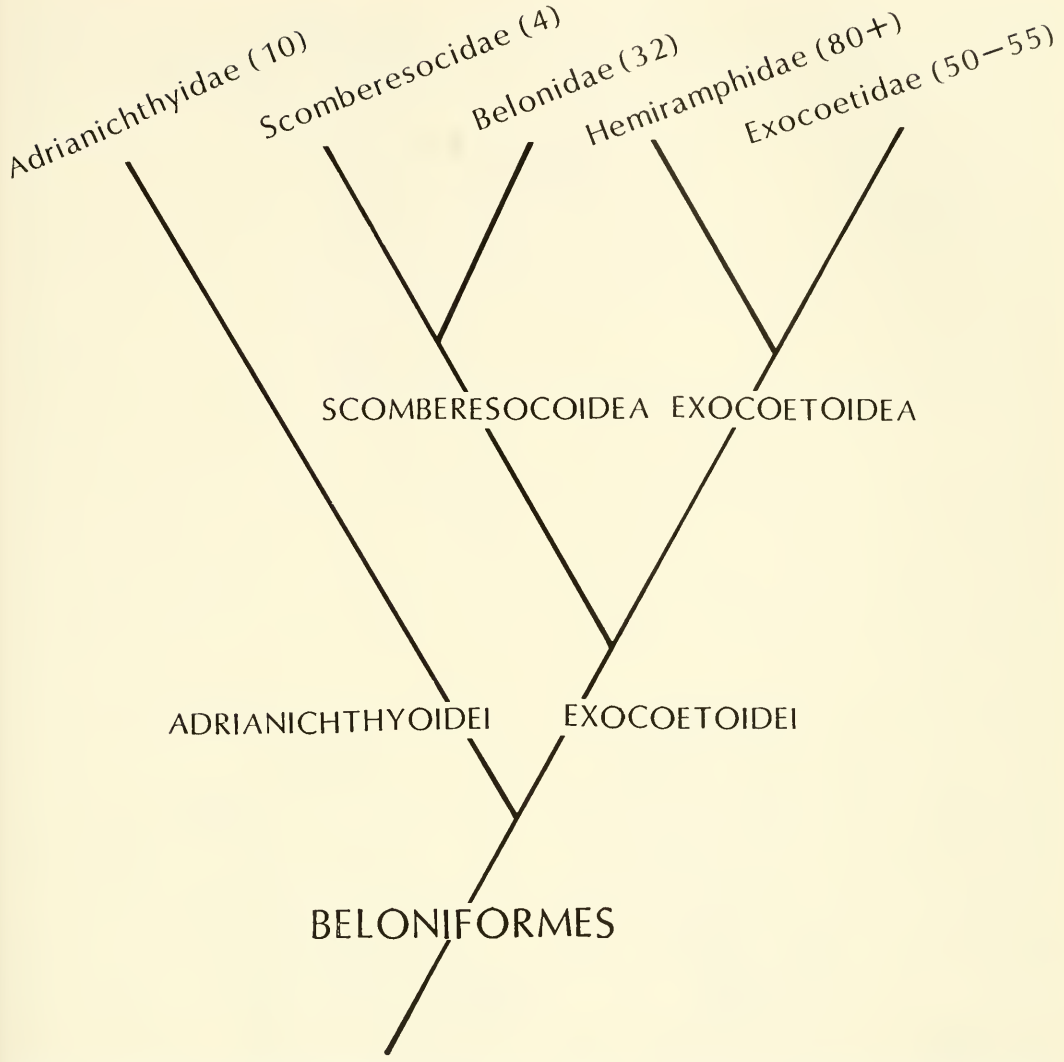


Figure 7. Cladogram of beloniform relationships, modified after Collette *et al.*, 1984. The numbers in parentheses after family names indicate number of included species.

socid), or entirely absent (exocoetid) in beloniforms. Before summarizing the principal components of this specialized labroid pharynx it is necessary to consider one further feature of the PJA.

Liem (1973) first drew attention to a fundamental difference in the muscular linkage between LPJ and neurocranium in cichlids as compared to other taxa (see also Liem, 1986). As part of the morphological basis for the adaptive radiation within the Cichlidae, Liem (1973) identified a functionally strategic shift in the insertion of the fourth levator externus muscle (le4) from the fourth epibranchial bone to the LPJ. A similar shift in levator insertion has since been found in labrids (including scarids and odacids) and embiotocids (Liem and Greenwood, 1981; Liem and Osse, 1975; Stiassny, 1980), and

the presence of this muscle sling has been thought to be central to the functional innovation of these taxa as well as being synapomorphic for the three families (Kaufman and Liem, 1982; Liem and Greenwood, 1981). The pomacentrids were thought either to entirely lack the le4/LPJ linkage (Liem and Greenwood, 1981) or possess a muscular sling in "its most primitive and incomplete configuration" (Liem, 1986: 311; see also Kaufman and Liem, 1982).

Our observations of the muscle sling in the Pomacentridae reveal a considerable amount of variation within that clade. In some taxa (e.g., *Neopomacentrus*, *Chromis* and *Amphiprion*; Fig. 8C) the configuration is much like that of other non-labroid percomorphs (e.g., Fig. 8A). While in others (e.g., *Stegastes*, *Dascyllus*, *Pomacentrus* and *Abudefduf*; Fig. 8B) the fibres of le4 are continuous, although interrupted by a fine myosept (see also Liem, 1986; Fig. 4 for the presence of a similar myosept in *Embiotoca*), with those of a division of the obliquus posterior. In those taxa in which the muscle sling is particularly well-developed (e.g., *Abudefduf* and *Stegastes*) the compound le4/obliquus posterior can be easily dissected free of the fourth epibranchial revealing a continuous connection between the neurocranium and LPJ, i.e., a true muscle sling.

From gross anatomical dissection it is not possible to determine exactly which components of the obliquus posterior muscle are incorporated into the compound muscle sling, and we have not undertaken an analysis of the ontogenetic transformations resulting in the compound muscle of pomacentrids. In view of this, the question of the homology of the resultant system with that of cichlids (Aerts, 1982; Claeys and Aerts, 1984), labrids and embiotocids (Liem, 1986; Liem and Sanderson, 1986) must remain open. The fact that a muscle sling is present only in some pomacentrid species poses problems for the analysis of this character at the level of the Labroidei.

Two possible interpretations suggest themselves based on this character distribution: 1) the pomacentrid muscle sling has been derived independently from that of the remaining labroids, or 2) a muscle sling is primitive for the Labroidei as a whole and has subsequently been lost within the Pomacentridae. Further information regarding the intrarelationships of the Pomacentridae may help resolve this question. For example, if the presence of a muscle sling within the Pomacentridae is found to characterize groups congruent with those characterized by other characters, a case could be made for suggesting the muscle sling developed within that clade. If, alternatively, the presence of a muscle sling is in conflict with the distribution of other characters and the absence characterizes corroborated groupings, absence could be considered as the derived condition. Lacking a precise knowledge of the intrarelationship of pomacentrid clades and based on the absence of a muscle sling in other pharyngognathous perciforms, we tentatively favor the second alternative and suggest that the muscle sling is indeed primitive for the Labroidei. However, we freely acknowledge that this is a relatively weak assumption and that future work may support alternative interpretations.

A remarkable similarity exists between the labroid muscle sling and that of exocoetid beloniforms (compare Figs. 2E and 9A or B). In the latter group the le4 (and a small slip of the levator posterior muscle) merges with a division of the obliquus posterior and inserts onto the LPJ, thus morphologically (and presumably also functionally) simulating the labroid configuration in remarkable detail. A similar muscle sling is not developed in the scomberesocids (Fig. 2D), and in these taxa a well-developed obliquus posterior and a fifth adductor connect the LPJ with the dorsal elements. The le4 and levator posterior both insert onto the head of the fourth epibranchial, and no fibers pass below it.

Quite apart from the striking suite of (homoplastic) morphological similarities

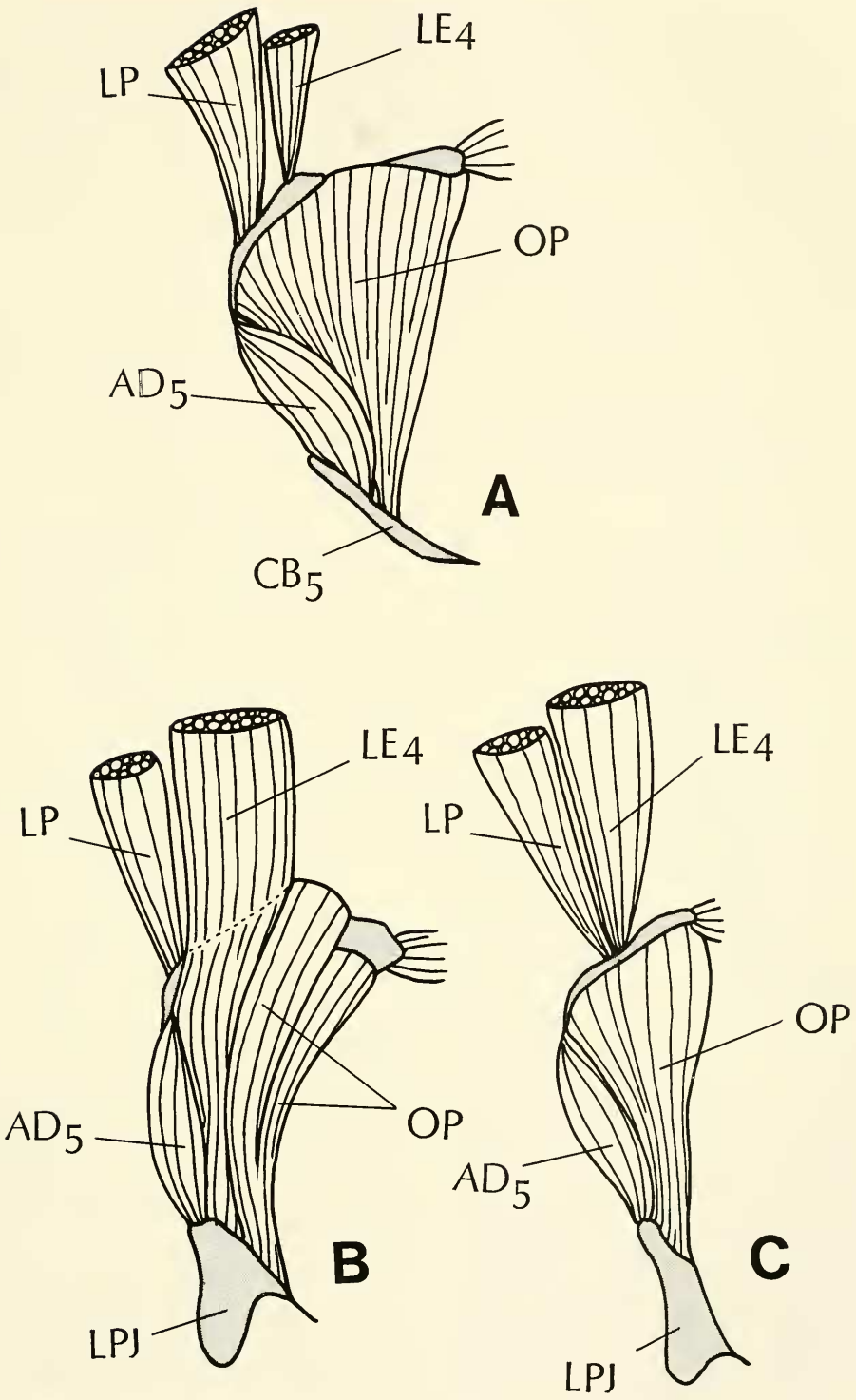


Figure 8. Isolated pharyngeal "muscle sling" components in: A. *Percichthys*; B. *Stegastes*; C. *Chromis*.

between the PJAs of exocoetids and labroids, these two lineages (as well as the scomberesocids) differ from other taxa in that *all* members possess the pharyngognathous condition of functionally united fifth ceratobranchials, regardless of the diet of each species. In other families the expression of pharyngognathy is limited to only a few (presumably duraphagous) members of each lineage, and is repeatedly correlated with an overall pharyngeal hypertrophy. The labroid pharyngeal synapomorphies (and the similar, but independently derived, beloniform ones) are not simply correlated with a durophagous diet; these taxa bear the synapomorphies regardless of the particulars of diet and trophic modification peculiar to individual species.

As indicated by the above discussion, the possession of united fifth ceratobranchials, i.e., pharyngognathy, is actually quite mosaically distributed among perciforms and at this level at least, is not indicative of any close phylogenetic relationship between the taxa in which it occurs. Thus, although it was originally in this context that the taxa comprising the Labroidei were considered to be closely related, the shared possession of the pharyngognathous condition is not itself the most compelling evidence for the monophyly of this clade. However, the fact that *all* labroid taxa, with the exception of *Cichla* (Stiassny, 1982), express united fifth ceratobranchials does suggest that this feature may have some value in uniting the Labroidei. While it is true that most labroids have a hypertrophied PJA capable of a powerful pharyngeal bite (Liem and Greenwood, 1981), this is by no means universal within the clade (e.g., Emery, 1973; Stiassny, 1982; Yamaoka, 1978). Nevertheless, even those labroids with extremely weak pharyngeal development exhibit the pharyngognathous condition of fused fifth ceratobranchials. Such universality of pharyngognathy, in the face of considerable pharyngeal variation, is unique among perciforms, and we consider this to be an indication that structural and functional union of the fifth ceratobranchials is primitive for the Labroidei and that its presence in forms with poor pharyngeal development merely reflects a retention of the primitive condition.

The Labroidei can thus be diagnosed on the basis of the presence of the following configuration of the pharyngeal jaw apparatus:

1. A LPJ with a well-developed ventral keel, onto which is inserted a portion of the transversus ventralis IV muscle.
2. A true diarthrosis between the UPJ and neurocranial apophysis.
3. A neurocranial apophysis of characteristic ventrally projecting and rounded form.
4. Presence of a m. transversus pharyngobranchialis 2 division of the transversus anterior muscle complex (secondarily reduced in the Embiotocidae). This character is somewhat ambiguous (see discussion on page 276).
5. An undivided sphincter oesophagi muscle.
6. A muscle sling directly suspending the LPJ from the neurocranium (polymorphically expressed within the Pomacentridae). See page 284 for a discussion of this character.
7. A structural union of the LPJ even in the absence of pharyngeal hypertrophy and functional duraphagy.

The interesting preponderance of characters concerning the pharyngeal jaw apparatus in labroid systematics is discussed further on pages 306–308. In the course of this investigation a further character of the pharyngeal region (although not obviously functionally related to the PJA) has been identified, and before concluding this section on labroid monophyly that character is discussed.

As already noted, extensive data exist on the configuration of dorsal branchial arch elements in acanthomorph fishes, but considerably less is known about variation in the ventral branchial elements. Fortu-

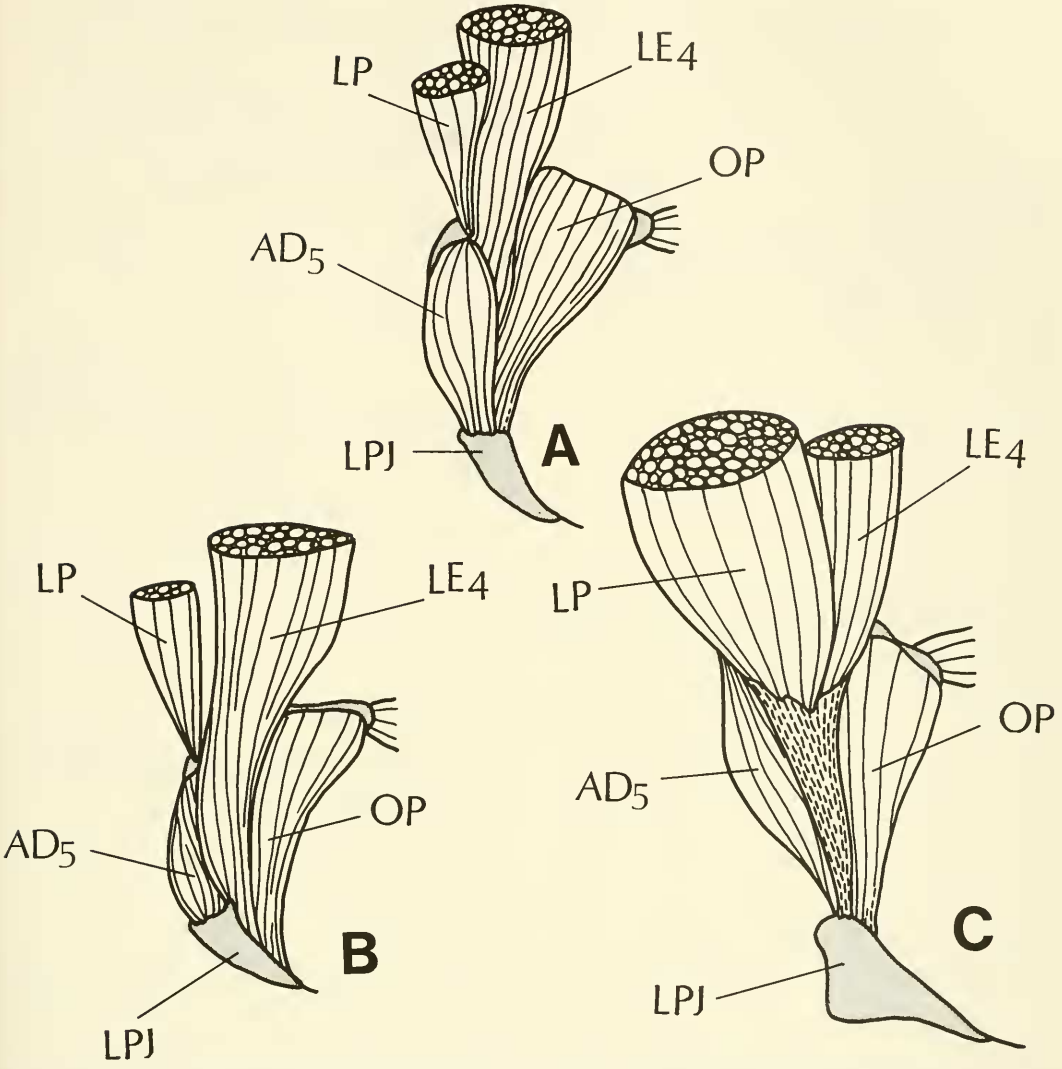


Figure 9. Isolated pharyngeal "muscle sling" components in: A. *Astatotilapia*; B. *Ditrema*; C. *Labrus*.

nately some comparative data are available (e.g., Nelson, 1967a, 1969; Travers, 1984a,b). Investigation of the configuration and associations of the ventral branchial arch elements of labroid fishes renders several features that may be potentially useful in resolving labroid intrarelationships (page 296).

In addition to these features, a particular configuration of basibranchial elements characterizes the entire Labroidei. In labroids the first basibranchial is an elongate, cylindrical element situated partially below the axis of the basihyal and the remaining elements of the basibranchial series (Figs. 10A–E). Although there is considerable variation in this osteological complex, the first basibranchial does not lie below the axis of the basihyal and remaining elements in the majority of outgroup taxa examined. In most outgroup taxa, rather, the first basibranchial is a lat-

erally compressed, almost square element and the basihyal/basibranchial series are more or less horizontally aligned with the first basibranchial abutting the caudal margin of the basihyal element (Fig. 10D; Nelson, 1967a, 1969; Travers, 1984a,b). Among outgroups a similar configuration was found only in the girellid, *Girella*.

In view of its limited distribution, *the presence of an elongate, cylindrical first basibranchial element ventrorostrally displaced to lie partially below the basihyal axis is interpreted as an additional synapomorphy uniting the labroid clade*, and the presence of similar modifications in *Girella* is presumed to be homoplasous.

In summary, the monophyly of the Labroidei seems to have been established beyond any reasonable doubt. Seven of the eight characters used in the definition of the assemblage are features of the pharyngeal jaw apparatus, and the eighth (i.e., the basibranchial character described above), although not obviously implicated in the PJA, is also a character of the pharyngeal region. Despite a conscious and concerted effort to locate synapomorphies in other structural (functional) systems, the weight of evidence for labroid monophyly remains in the pharynx (see discussion on pages 306–308).

LABROID INTRARELATIONSHIPS

Character Survey

In this section we review the various characters that have been used in previous analyses of labroid intrarelationships, and present novel data. For ease of description, the characters are arranged into rather loosely defined morphological units wherever possible; otherwise they are simply listed independently. Where appropriate each character or character complex is introduced with a short review of the relevant comparative literature and any problems surrounding past usage of terms or identification of homologies are discussed. As in the preceding section, summary statements of characters assessed to be synapomorphic for labroid clades are italicized for ease of reference.

Characters of the Pharyngeal Jaw Apparatus

LPJ Union and Medial Tooth Implantation. As we mentioned, within the Labroidei two modes of LPJ union are expressed. In cichlids the two fifth ceratobranchial elements are united medially in a caudally convoluted and interdigitating suture (Fig. 3B), and the pharyngeal teeth on the corresponding toothplate can be divided into left and right regions with no teeth located over the symphysis of the two bones. Regarding the retention of a sutural union, and the tooth implantation pattern, we agree with Kaufman and Liem (1982) that the cichlid arrangement represents the plesiomorphic labroid condition. In contrast, the condition in adult labrids, pomacentrids and embiotocids is a complete fusion of the two LPJ elements and no trace of the central suture remains (Figs. 3A, C, D). Tooth rows are arranged radially across the LPJ, and teeth are located over the median region of the jaw (Kaufman and Liem, 1982).

Because a similarly derived arrangement is found nowhere else among pharyngognath percomorphs, contrary to Kaufman and Liem (1982), we interpret *the total obliteration of all traces of a sutural union of the two fifth ceratobranchial elements of the LPJ and the implantation of pharyngeal teeth over the midline of the bone to be synapomorphies uniting the labrid embiotocid and pomacentrid radiations.*

Pharyngo-Cleithral Joint. Liem and Greenwood (1981), and later Kaufman and Liem (1982) described what they termed "pharyngo-cleithral joints" in labrid and pomacentrid taxa. The latter authors were of the opinion that the joints in these two lineages are "clearly dissimilar in form" but offer little in the way of substantiation of the claim. The pharyngo-cleithral joint is listed as one of the synapomorphies

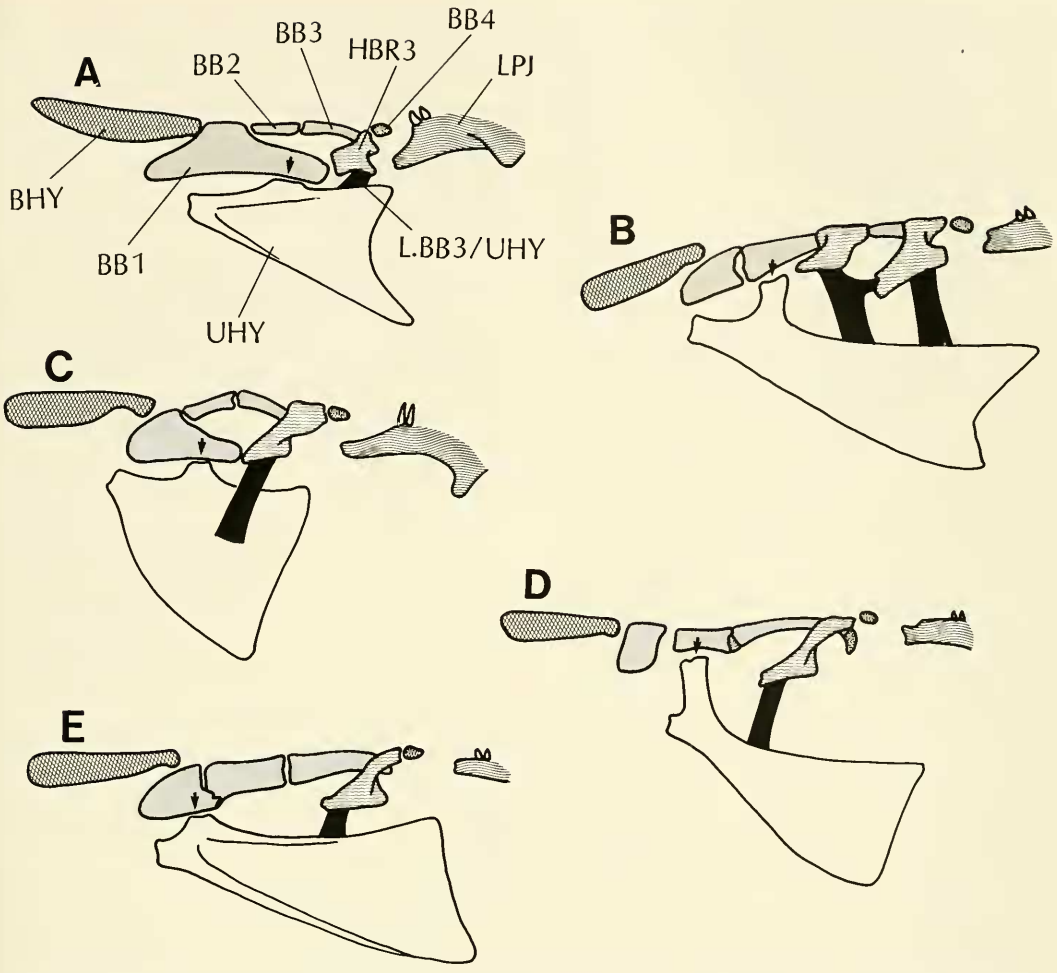


Figure 10. Ventral branchial arch elements in: A. *Labrus*; B. *Astatotilapia*; C. *Pomacentrus*; D. *Percichthys*; E. *Embiotoca* in lateral view.

characterizing the Labridae (Kaufman and Liem, 1982: 9), and Liem and Sanderson (1986) investigated the function of the joint during pharyngeal mastication. Lauder and Liem (1983: 169) cited the presence of a "pharyngo-cleithral articulation of characteristic form" as a synapomorphy of the Pomacentridae. Our observations of the pharyngeal-cleithral associations in various pomacentrid (Fig. 11A) and labrid (Figs. 11B, C) taxa are somewhat at odds with those of these previous investigators and lead to a different conclusion regarding the phylogenetic significance of the structural complex.

Among pomacentrids there is considerable variation in the degree to which the expanded lateral horn of the LPJ (=muscular process of Liem, 1973) contacts the cleithrum. In some taxa (e.g., species of *Microspathodon* and *Chromis*) there is no contact and a pharyngo-cleithral articulation is consequently lacking. In others (e.g., species of *Stegastes* and *Pomacentrus*) the area of contact is extensive and similar to that of many labrids.

Among labrids also there is considerable variation in the degree of pharyngo-cleithral contact and, although contact is always established (even in those forms with greatly reduced PJAs), the actual articulation surface may be extremely small (e.g., Fig. 11C). A distinct articular process (fossa?) on the cleithrum, and the consequent development of a true synovial joint (Liem and Greenwood, 1981) are not present in all labrids; in fact the development of such a joint appears to be present only in scarids and odacids (Kaufman and Liem, 1982: fig. 6). In our opinion the morphological differences between labrid (possibly excluding scarids and odacids) and pomacentrid pharyngo-cleithral articulations are quantitative and not qualitative as implied by Kaufman and Liem (1982). What is strikingly similar in these two taxa, however, is the form of the LPJ.

LPJ Form. Representative labroid LPJs are illustrated in Figure 3. Within each of the labroid families there exists a considerable range in both the relative size and shape of the LPJ. This is perhaps least marked in pomacentrids (Emery, 1973) and embiotocids (De Martini, 1969), but in labrids (Gomon and Paxton, 1986; Yamaoka, 1978) and cichlids (Fryer and Iles, 1972; Pellegrin, 1903) the range is truly remarkable. Despite intralineal variation and a number of autapomorphic features (Stiassny, 1980), the labrid and pomacentrid LPJs all share a markedly similar facies. These similarities are rather difficult to quantify precisely; however, they are easily appreciated by a comparison of each of the jaws illustrated in Figure 3. *The labrid/pomacentrid jaw is highly characteristic in being almost Y-shaped, rather than essentially triangular, with an emphasis upon the long lateral horns that are distally expanded. Uniquely in labrids and pomacentrids, LPJ width is greater than (rarely equal to) the LPJ length; this relation is reversed in other taxa. The elongation of the LPJ lateral horns and their distal expansion are synapomorphic features of the labrid and pomacentrid LPJ*; they are also a structural prerequisite for the development of a pharyngo-cleithral association. As pointed out above, although not strictly a character for use in our analysis, the development of a pharyngo-cleithral articulation in labrids, and its tendency for expression in the pomacentrids, is clearly correlated with these LPJ specializations.

LPJ Muscle Sling. Liem and Greenwood (1981) distinguished between a cichlid/embiotocid type of muscle sling on the one hand and a labrid type on the other. In the former, the fourth levator externus muscle is morphologically and functionally dominant during pharyngeal mastication, while in the Labridae it is the levator posterior muscle that is the dominant element (see also Liem, 1986; Liem and Sanderson, 1986; Yamaoka, 1978). Dominance of the fourth levator is considered by Liem and Greenwood (1981) to be part of an unique, specialized complex characterizing the Cichlidae-Embiotocidae lineage, while dominance of the levator posterior, forming a force couple with the pharyngocleithralis externus muscle, is considered by Kaufman and Liem (1982) to be one of the synapomorphies characterizing the Labridae.

It seems most probable that a structural and functional dominance of the fourth levator is the primitive condition of the labroid muscle sling for two reasons: in Pomacentrids the levator posterior never contributes to the muscle sling, and in outgroup taxa the levator posterior is invariably smaller and less well-developed than the fourth levator externus. The highly complex and elaborate muscular sling of the Labridae (Kaufman and Liem, 1982; Liem and Sanderson, 1986) is correctly interpreted as an autapomorphy of that clade.

Stiassny (1980) proposed that a caudad migration of the levator posterior origin away from the "lateral awning" (Barel *et al.*, 1976) on the ventral face of the pterotic or intercalar bone is a synapomorphy uniting the Embiotocidae and Labridae.

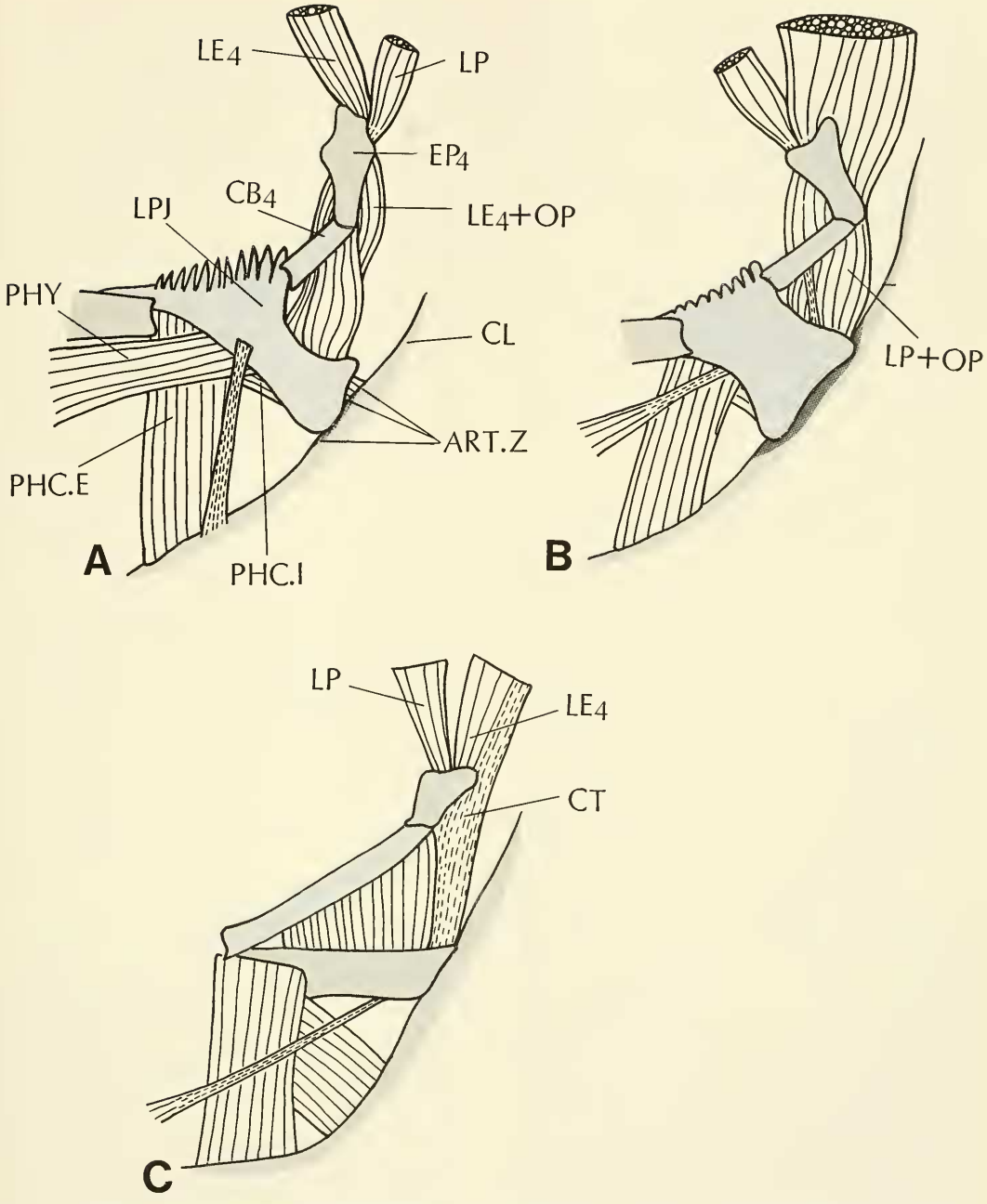


Figure 11. Pharyngo-cleithral associations in: A. *Eupomacentrus*; B. *Labrus*; C. *Labroides dimidiatus*.

Our reinvestigation of this character fails to reveal any significant differences between the location of levator insertion sites in pomacentrids, cichlids and embiotocids. Within the Labridae an extremely wide range of sites are encountered and based upon these Yamaoka (1978) has constructed a morpho-ecological classification of labrid types.

UPJ Composition. The structure of the dorsal gill arches has figured prominently in studies of euteleostean relationships (e.g., Nelson, 1969; Rosen, 1973), and a number of dorsal gill arch characters have direct bearing on relationships within the Labroidei (Kaufman and Liem, 1982; Liem and Greenwood, 1981; Nelson, 1967a; Stiassny, 1980, 1981). A summary of plesiomorphous osteological and myological features of the perciform upper pharynx is given by Stiassny (1981, 1982).

Upper Pharyngeal Toothplates. Compared with the modal perciform arrangement (Stiassny, 1981), within the Labroidei reduction of a number of features of dorsal gill arch osteology is evident. *In the Embiotocidae (Figs. 12B, 13B) and Labridae (Fig. 12D) the second pharyngobranchial is reduced to a slender, rod-like element with no trace of a second pharyngobranchial toothplate* (Nelson, 1967a). This condition stands in contrast to that seen in the Cichlidae (Fig. 12A), the Pomacentridae (Fig. 12C), and the majority of outgroups, in which the second pharyngobranchials are robust elements each bearing a well-developed toothplate.

Loss of the second pharyngobranchial toothplates occurs elsewhere within the Percomorpha, most notably among the Blenniidae (Springer, 1968), in which the entire second pharyngobranchial is absent and only a single toothbearing element (pharyngobranchial 3 and 4?) is present. In a single mastacembelid lineage the second pharyngobranchial is reduced to a small cartilage (Travers, 1984b). Despite the occassional loss of the second pharyngobranchial toothplate elsewhere within the Percomorpha (Stiassny, 1981), we consider the absence of this structure in the Embiotocidae and Labridae to be evidence suggestive of a sistergroup relationship between them.

As in the Euteleostei generally, the paired third pharyngobranchial elements (and associated toothplates) comprise the major component of the upper pharyngeal jaw in labroids (Nelson, 1967a, 1969). In the Cichlidae (Fig. 12A) and Pomacentridae (Fig. 12C) the fourth upper toothplates also contribute significantly to the composition of the UPJ, and are suturally united to their respective third pharyngobranchials. Typically among outgroup taxa the fourth upper toothplate is well-developed and cups around a cartilaginous fourth pharyngobranchial, although rarely it is as intimately associated with the third pharyngobranchial or as highly ossified as in cichlids and pomacentrids (Stiassny, 1981).

In embiotocids Up4 is a fragile, weakly ossified element with feebly developed teeth and relatively little common border with its associated third pharyngobranchial (Fig. 12B). In the Labridae no evidence remains of an independent Up4 (Fig. 12D; see also Nelson, 1967a, 1969). *We consider the reduction of the Up4 element in the upper pharyngeal jaw to be a synapomorphy of these two labroid taxa.* Ontogenetic data may clarify the nature of the reduction of this character within the Labridae.

The families Cichlidae and Embiotocidae share a cartilaginous cap on the anterior border of the second epibranchial (Fig. 14) (Stiassny, 1981). However, reinvestigation of this character leads us to consider this condition non-homologous between the two families. Within the Cichlidae, the second epibranchials bear an expansion rostrally with a cartilaginous cap. This cartilaginous flange does not articulate with any other pharyngeal element, and extends forward into the buccal cavity forming the core of pharyngeal pad developed on the mouth roof (Trewavas, 1973). In addition, the head of the epi-

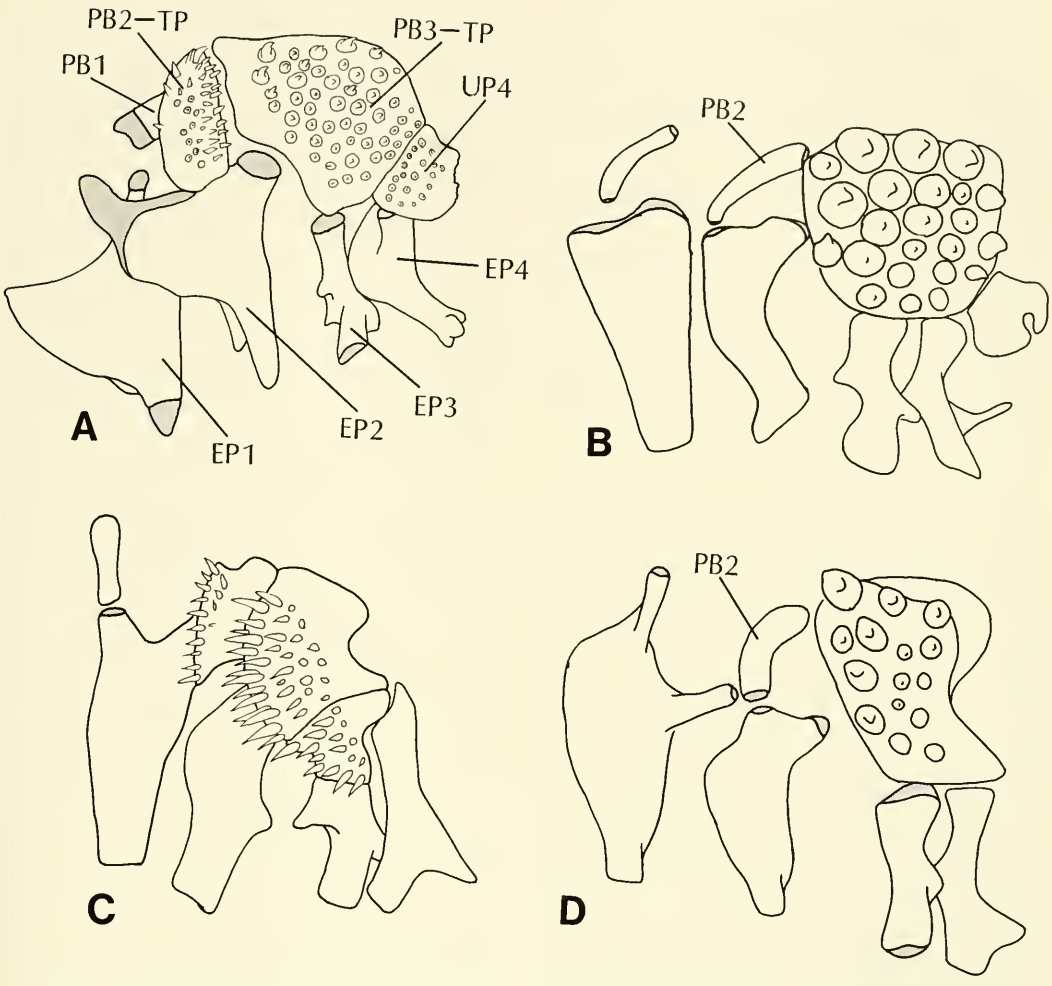


Figure 12. Right upper pharyngeal jaw in ventral view. A. *Geophagus*; B. *Micrometrus*; C. *Stegastes*; D. *Labrus*.

branchial bears two other cartilaginous pads, corresponding to its points of articulation with pharyngobranchials 2 and 3 (Fig. 14A). Within the Embiotocidae, only those cartilaginous pads associated with the pharyngobranchial articulations are present (Fig. 14B), either continuous with each other or separated by a narrow gap. Because the cartilaginous extension on the anterior border of the second epibranchial has no counterpart in the Embiotocidae, in terms of either form or topographic relationship to the adjacent elements, we do not consider this similarity to be indicative of a close relationship between the two families.

Interarcual Cartilage Development. The presence of a cylindrical rod-like interarcual cartilage connecting the uncinate process of the first epibranchial element with a dorsal process of the second pharyngobranchial is considered by Rosen and Greenwood (1976) to be a synapomorphy uniting the Perciformes. In a subsequent review of the morphology and distribution of this structure Travers (1981) concluded that an interarcual cartilage (of some form) is primitively present in a wide

range of ctenosquamate taxa (see also Rosen, 1985).

Among outgroup taxa investigated here a rod-like interarcual cartilage is typically present. Although a well-developed interarcual cartilage is present in most sciaenid and gerreid taxa examined, an interarcual cartilage is lacking in both pharyngognaths *Pogonias cromis* and *Gerres poeti*. Within the Perciformes the interarcual cartilage has apparently been lost independently a number of times (e.g., Springer, 1968; Travers 1981, 1984a). Johnson (1984) listed the presence or absence of an interarcual cartilage in representatives of all percoid families.

Within the Labroidei, a rod-like interarcual cartilage is fully developed in the Pomacentridae (Fig. 13C), reduced or absent among the Cichlidae (Fig. 13A; see also Stiassny, 1981), and completely absent in both the Labridae (Fig. 13D) and Embiotocidae (Fig. 13B). The cichlid condition is complex as an interarcual (present as a nubble of cartilage suspended in a connective tissue strand) occurs in many Neotropical and Madagascan lineages but is present only very rarely as an individual anomaly in the more derived African lineage (Stiassny, in press). As the Cichlidae is polymorphic for this character we tentatively consider the cartilage to be primitively present, but reduced in the family, perhaps having been lost independently several times within the clade. *The complete absence of an interarcual cartilage is interpreted as a synapomorphy of the Labridae and Embiotocidae.*

Stiassny (1980) cited the loss of a well-developed anterodorsal process on the second pharyngobranchial (primitively accommodating the medial end of the interarcual cartilage) as a synapomorphy uniting the Labridae, Embiotocidae and Cichlidae. Reexamination of this character fails to corroborate that assessment. Comparison of second pharyngobranchial morphology in a range of cichlid and pomacentrid and additional outgroup taxa does not reveal any significant difference in the degree of development of this process in these taxa. The fact that the process is lacking on the second pharyngobranchials of labrids and embiotocids is clearly related to the overall reduction of the elements in these taxa.

With regard to branchial osteology, the monotypic family Pholidichthyidae mirrors the Labridae (and in some respects other labroids also) to a remarkable extent. *Pholidichthys* lacks a cartilaginous fourth pharyngobranchial, a fourth upper toothplate, epibranchials 3 and 4 articulate with the third pharyngobranchial, no interarcual cartilage is present and the second pharyngobranchial lacks a toothplate and anterodorsal process (Springer and Freihofer, 1976). In addition the fifth ceratobranchials of *Pholidichthys* are also united into a single element. Unfortunately no specimens of this genus were available to us for dissection so we are unable to comment on the condition of the branchial myology of these fishes. An investigation of their myological configuration is particularly interesting with regard to the possible development of a pharyngeal muscle sling in these taxa. (See discussion of beloniform/labroid pharyngeal parallels on pages 274–286.)

Additional Characters of the Pharyngeal Region

Ventral Branchial Myology. In a phylogenetic context, teleostean ventral branchial myology has received far less attention than the corresponding dorsal configuration. Although much information is available in papers describing the myology of various individual taxa, few comparative data have been assembled with a view to resolving problems of phylogenetic relationship. The works of Dietz (1921), Nelson (1967b), Winterbottom (1974) and Lauder (1983) are notable exceptions and provided much valuable comparative information. Goedel (1974a,b) and Anker (1978) also provided useful data on the ventral branchial mus-

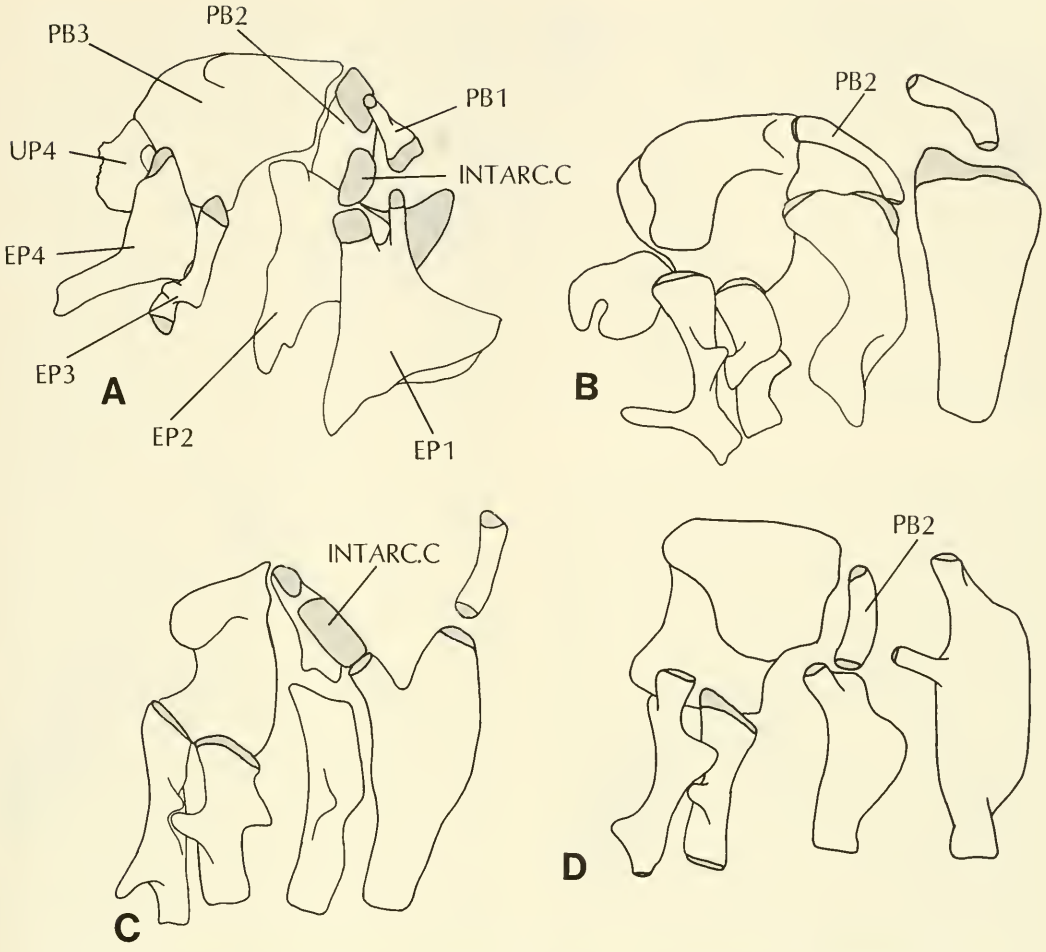


Figure 13. Right upper pharyngeal jaw in dorsal view. A. *Geophagus*; B. *Micrometrus*; C. *Stegastes*; D. *Labrus*.

cles of two African cichlid fishes, and characters of the ventral branchial musculature of labroids are employed by Stiassny (1982, and in press) and Greenwood (1985).

The plesiomorphic perciform configuration of ventral branchial muscles is represented here by the arrangement in *Morone* (Fig. 4A). Both the rectus ventralis IV and obliquus ventralis IV insert together onto a well-developed semicircular ligament system. Among labroids a similar configuration is present in embiotocids (Fig. 4B) and most cichlids (Fig. 4C; Greenwood, 1985 and Stiassny, in press), as well as in the percoid outgroups examined (*Serranus* lacks the semicircular ligament system entirely [Stiassny, in press]).

In labrids (Fig. 4D) and pomacentrids (Fig. 4E) the rectus IV and obliquus IV muscles insert independently on the semicircular ligament. Although a seemingly minor distinction, these insertional differences consistently appear to differentiate labrids and pomacentrids from the other perciform taxa examined, and as such are interpreted as synapomorphic for the two lineages.

Primitively among acanthomorphs a

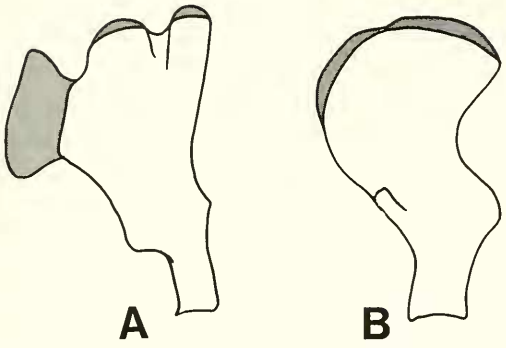


Figure 14. Isolated second epibranchial element. A. *Astatotilapia*; B. *Cymatogaster*.

single ligament passes from the third hypobranchial element of either side to attach to the dorsal surface of the urohyal (ligamentum urohyale caudale of Anker, 1978). Uniquely in the Cichlidae (Fig. 10B) an additional ligament (ligamentum urohyale intermedium of Anker, 1978) passes from the second hypobranchial element of either side to attach to the dorsal surface of the urohyal somewhat in advance of the caudal ligament. A similar elaboration of a ventral branchial ligament system is lacking in all other taxa and is identified as an additional synapomorphy uniting the members of the Cichlidae.

Ventral Branchial Osteology. There exists a large body of data on the configuration of dorsal branchial osteology, but as with the myology of the region, less is known of the variation in the ventral branchial elements. Some comparative data are available (e.g., Nelson, 1967a, 1969; Travers, 1984a,b) and these provide useful additional outgroup data.

In labrid (Fig. 10A), pomacentrid (Fig. 10C) and embiotocid (Fig. 10E) taxa the urohyal articulates via its dorsal process with the ventral surface of the first basibranchial element. This is not the case in cichlids (Fig. 10B), nor in the majority of percoid outgroups examined (e.g., Fig. 10D) where the urohyal articulates with the second basibranchial (occasionally at the cartilaginous junction of the first and second basibranchials).

Gerres and *Eucinostomus* provide exceptions to the above generalization and in these taxa the urohyal (although lacking a distinct dorsal process) articulates directly with basibranchial one. A similar association is present in the majority of Asian (but not African) mastacembelids and synbranchids (Travers, 1984a,b).

Despite these few mosaic occurrences, in the overwhelming majority of acanthomorph taxa the urohyal articulates with the second basibranchial, and the occurrence of *a basibranchial one/urohyal association in labrids, pomacentrids and embiotocids is interpreted as a synapomorphy uniting these three taxa.*

In labrids and pomacentrids (Figs. 10A, C) the urohyal articulates with a large keel-like caudally directed ventral extension developed on the elongate cylindrical first basibranchial element. Primitively among perciforms the first basibranchial is a deep, almost square element that lacks a ventral process (e.g., Fig. 10D). In cichlids and embiotocids the first basibranchial is also somewhat elongate and cylindrical and varies in size. A well-developed caudally directed ventral process, however, is never developed in the manner or extent approaching that of the pomacentrids and labrids.

The mastacembelid and synbranchid lineage described by Travers (1984a,b) prove exceptional among outgroups in the possession of well-developed ventral processes on the first basibranchial.

Despite the occurrence of a similar basibranchial morphology in the labrid/pomacentrid pair and in the distantly related symbranchid/mastacembelid lineage, the labrid/pomacentrid basibranchial configuration is interpreted as a synapomorphy uniting these two taxa.

Caudal Fin Skeleton. Extensive literature exists on the systematic value and distribution of variation in caudal structure within the Acanthomorpha (e.g., Ford, 1937; Gosline, 1961; Hollister, 1936, 1937;

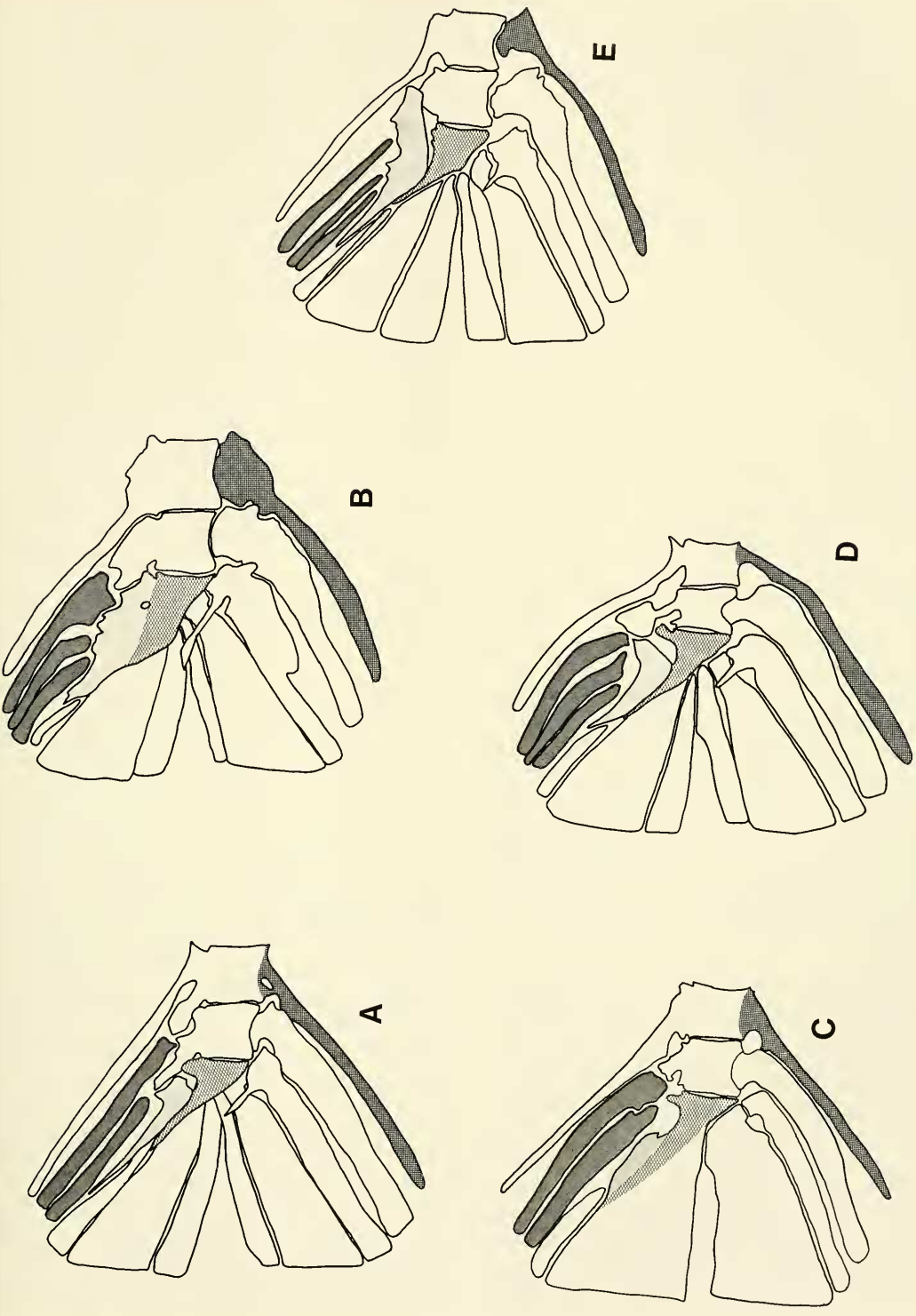


Figure 15. Caudal skeleton of: A. *Cichla*; B. *Stegastes*; C. *Labrus*; D. *Embiotoca*; E. *Percichthys*.

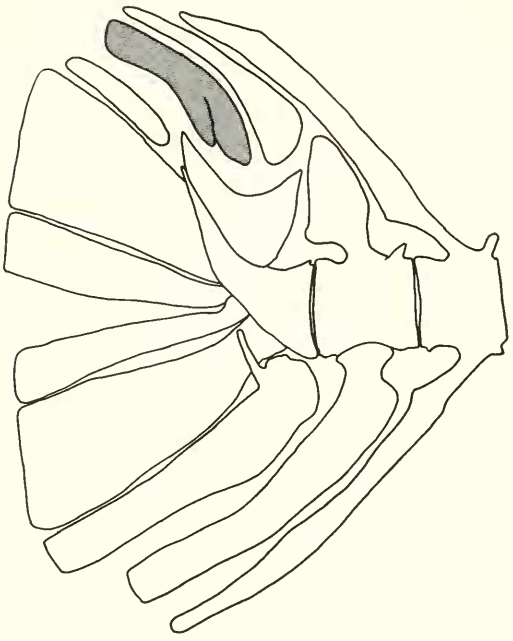


Figure 16. Caudal skeleton of A. *Hysterocarpus* (40 mm SL).

Johnson, 1984; Patterson, 1968; Rosen, 1973; Rosen and Patterson, 1969). The basal perciform caudal skeleton has been described by Gosline (1961) as having three epurals, two independent uroneural ossifications, and the hemal arches on the penultimate and antepenultimate vertebrae autogenous. Patterson (1968) further characterized the basal Perciform caudal skeleton as having, among other features, a low neural crest on the penultimate vertebrae.

Epural Reduction. In labrid (Fig. 15C; see also Ford, 1937) and cichlid (Fig. 15A; see also Vandewalle, 1973) taxa there are two epural bones in the caudal skeleton. Among perciforms the primitive condition, as found in the Embiotocidae (Fig. 15D), Pomacentridae (Fig. 15B), and most of the outgroup taxa examined (e.g., Fig. 15E), is the possession of three epurals (see also Gosline, 1961). Although exceptional among embiotocids, individuals of *Hysterocarpus* (Fig. 16) and *Micrometrus* are occasionally found with only two independent epurals. In these individuals the anomaly appears to be the result of fusion. In young *Hysterocarpus*, three separate epurals are present, whereas in the adult these are occasionally united along a portion of their border. The labrids and cichlids bear no trace of a third epural at any time during ontogeny.

Despite the somewhat mosaic distribution of epural reduction among phylogenetically disparate acanthomorph taxa (e.g., reduction occurs in a range of serranid lineages as well as in a number of "paracanthopterygians" [Rosen and Patterson, 1969]), three epurals is undoubtedly the primitive condition for percomorphs (Patterson, 1968). In view of this *we interpret the reduction of epural number in the Labridae and Cichlidae as a synapomorphy uniting the two clades.*

Uroneural Ossification. In common with a range of perciform taxa, the labroid caudal skeleton has but a single uroneural ossification (Gosline, 1961). In the Embiotocidae and Cichlidae, the uroneural is autogenous, as it is in all outgroup taxa examined (e.g., Fig. 15E). Embiotocids differ from outgroups, however, in having the uroneural elements very closely applied to the urostyle (Fig. 15D); nonetheless the uroneural can easily be dissected free of the urostyle without damage to either element. In the Pomacentridae and Labridae the uroneural element is completely fused with the urostyle, resulting in a urostyle/uroneural block with no suture evident between the two elements (e.g., Fig. 15B). In labrids, hypurals 4 and 5 are also fused to the uroneural/urostyle block (Fig. 15C; see also Ford, 1937), a condition we consider to be synapomorphic for members of the Labridae.

Complete fusion of the uroneural with the urostyle, and the obliteration of all trace of a former sutural union, is interpreted as a synapomorphy uniting the pomacentrid and labrid clades.

Antepenultimate Vertebrae. Primitively among perciforms, the hemal arch of

the antepenultimate vertebra remains free from, although very closely associated with, its centrum (e.g., Fig. 15E; see also Gosline, 1961). Among labroids an autogenous hemal arch is also found in the Pomacentridae (Fig. 15B), where the hemal spine of the antepenultimate vertebra articulates with the centrum via a peg-like dorsal extension. The division between the two bones is clearly evident. Embiotocids, cichlids, and labrids exhibit a derived condition in having the hemal spine fused with the antepenultimate vertebra. Even in the early ontogeny of these elements (ca. 10 mm SL), there is no discernible division between these elements.

Although fusion of the antepenultimate centrum and hemal spine occurs in some other acanthomorph taxa (e.g., Gosline, 1961; Hollister, 1937; Springer, 1968), its absence in any of the perciform outgroup taxa examined in the course of our investigation leads us to consider this character as a synapomorphy uniting the labrids, embiotocids and cichlids.

Additional Characters

Subocular Shelf. The presence of a subocular shelf, usually formed by a medial extension of the third suborbital, is widespread among perciforms and appears to have been independently lost a number of times within this taxon (Smith and Bailey, 1962). Among the labroids the Pomacentridae and Embiotocidae have the subocular shelf, whereas the Cichlidae and Labridae do not. The markedly mosaic distribution of this character among outgroups renders polarity determination of the character extremely difficult. For example, a subocular shelf is absent in the Centrarchidae, Kyphosidae, Leiognathidae and Percidae, but is present in the Girellidae, Serranidae, and Sparidae. Even within the Gerreidae, this character is variable (Smith and Bailey, 1962). Clearly the subocular shelf has been lost repeatedly during perciform evolution. In the absence of a clearer knowledge of the precise relationships of the labroids to other perciform taxa, we are unable to determine the primitive labroid condition.

Endopterygoid Shelf. As noted by Stiassny (1980), primitively among acanthomorphs, the endopterygoid bone of the suspensorium bears a medially directed shelf forming the floor of the orbit. The adductor arcus palatini muscle inserts onto the endopterygoid shelf and, although the extent of adductor migration over the shelf varies (Rosen, 1973), insertion is invariably onto the lateral face of the bone.

In labrids and cichlids the medially directed endopterygoid shelf of other acanthomorphs is lacking, and the adductor arcus palantini inserts onto the medial face of the endopterygoid. The floor of the orbit now lacks a bony component and is instead entirely muscular. In both pomacentrids and embiotocids the endopterygoid shelf is well-developed and adductor insertion is onto its medial face.

Among all of the outgroup taxa investigated an endopterygoid shelf was lacking only in the single species of Mullidae examined. In this taxon the adductor also inserts onto the medial face of the bone and the floor of the orbit is entirely muscular. *In view of the extremely limited distribution of this feature within the Acanthomorpha, we interpret the loss of an endopterygoid shelf, and the subsequent migration of the adductor arcus palatini muscle from the lateral to the medial face of the endopterygoid, to be a synapomorphy of the Cichlidae and Labridae.*

Predorsal Bones. The structure and evolution of the predorsal bones have been extensively reviewed by Smith and Bailey (1961). Predorsals have generally been viewed as representing rayless pterygiophores (Smith and Bailey, 1961); however, it has recently been suggested that they are derived from neural arch material (P. Mabee, personal communication). Whatever their origin, variation in predorsal number is widespread and may be systematically useful at the present level of analysis.

The possession of three predorsal bones is the most common condition among the percoids (Johnson, 1984; Smith and Bailey, 1961) and, judging from the condition seen in most outgroup taxa, is primitive for the Labroidei as well.

Embiotocids and pomacentrids generally retain the primitive number of three predorsal ossifications, whereas the cichlids and labrids display a reduction in predorsal number. *The reduction in predorsal number, to two predorsals in the Labridae and to two or fewer in the Cichlidae, is considered to be a synapomorphy uniting these two families.*

Extrascapular Bones. Among percomorphs the extrascapular series of laterosensory canal bearing ossifications usually overlie the parietal region of the neurocranium. In those taxa in which the expaxial musculature has migrated onto the neurocranium the extrascapulars lie in the dermis superficial to the epaxial musculature (e.g, the Cichlidae). Uniquely among perciforms the extrascapulars have become fused with the parietals of embiotocids and pomacentrids. In these taxa the parietals each bear an open (or partially closed) tube running postero-laterally from the anterior parietal/supraoccipital border (Fig. 6C, D). *In agreement with Morris (1982) we consider the fusion of an extrascapular element with the parietal to be a synapomorphy uniting the Pomacentridae and Embiotocidae.* However, we are unable to corroborate Morris' assertion that a similar extrascapular/parietal fusion also characterizes the Scorpididae. In the representative scorpidid, kyphosid and girellid taxa investigated here, the extrascapular exhibited no particularly close association with the parietal bone of the neurocranium.

Epihemal Ribs. So-called epihemal ribs are developed in some or all representatives of the perciform families Embiotocidae, Pomacentridae, Cichlidae, Scorpididae, Girellidae, Chaetodontidae, Cirrhitidae, and Centrarchidae. Morris (1982) considered the presence of epihemal ribs as an indication that the pomacentrids (Fig. 17A) and embiotocids (Fig. 17B) bear a closer relationship to each other than either does to cichlids or labrids. However, a review of these structures indicates that the use of the term epihemal rib needs clarification because it describes two morphologically and developmentally distinct structures.

The epihemal ribs of pomacentrids (and scorpidids, girellids, chaetodontids and cirrhitids) are membranous ossifications extending into the horizontal septum between the epaxial and hypaxial musculature, and would thus appear to be modified intermuscular bones. The epihemals of embiotocids (and centrarchids, and a single cichlid species, *Geophagus surinamensis*) appear to be modified pleural ribs. We conclude that the epihemal ribs of embiotocids are distinct from those of pomacentrids, and that they in fact represent pleural ribs, for the following reasons: 1) The epihemal ribs of embiotocids do not extend into the horizontal septum, 2) they are preformed in cartilage as are pleural ribs (but not intermusculars, which are membrane bones and hence are no longer preformed in cartilage (Patterson, 1977)), and 3) the intermusculars and epihemals occur in overlapping series (Fig. 17B; contra Morris, 1982), indicating separate identity.

Although work in progress (Jensen) indicates that the arrangement of epihemal ribs may be informative at the intrafamilial level of analysis, lack of identity between pomacentrid and embiotocid epihemal ribs precludes support for Morris' (1982) statement of relationships based upon these structures. The morphological correspondence between the epihemal ribs of embiotocids and of the single species of cichlid fish is interesting; however, this similarity has little systematic significance.

Maxillary-Palatine Ligament. Stiassny (1980) described a ligament connecting the postmaxillary process of the maxilla with the palatine and ectopterygoid bones of

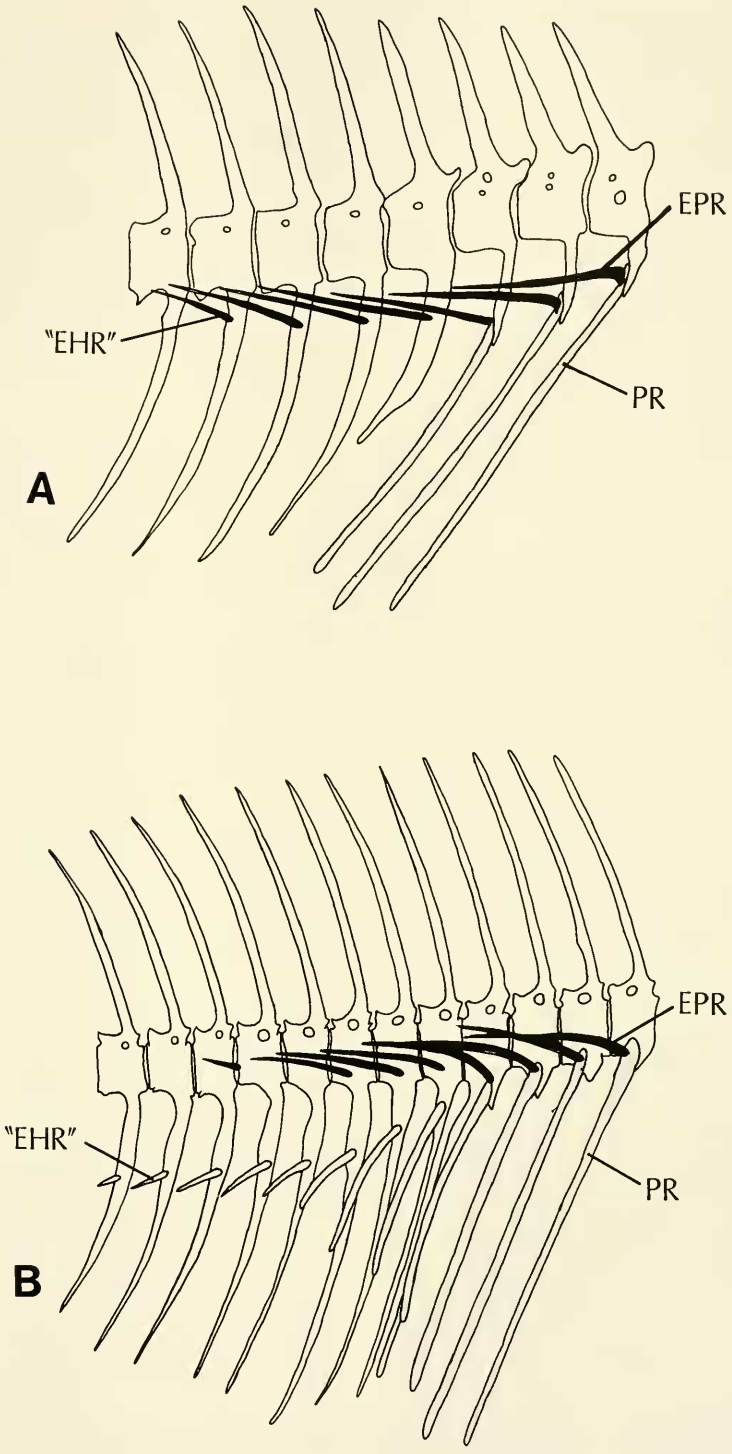


Figure 17. Epihemal ribs in: A. *Eupomacentrus*; B. *Embiotoca*.

the suspensorium as being a synapomorphy uniting the labrid and embiotocid lineages (see also Kaufman and Liem, 1982; Lauder and Liem, 1983). Our reinvestigation of this ligament fails to corroborate that assessment; the degree of development of the ligament varies markedly not only within other labroid taxa (e.g., a range of Neotropical and etropline Cichlidae possess a well-defined and discrete tract of connective tissue connecting the maxillae and palatine/pterygoid region), but also among a range of outgroup taxa examined during the course of this investigation. For this reason the presence of the ligament in labrids and pomacentrids is rejected as evidence of their close relationship.

tA_1 Insertion. Among percomorphs, and neoteleosts in general, control of the maxilla is achieved primarily through an insertion of the A_1 division of the adductor mandibulae muscle onto the posterior border of the maxillo-mandibular ligament, which runs from the lateral face of the maxilla to the lateral face of the angulo-articular (Rosen and Patterson, 1969; Stiassny, 1981). A tendon (tA_1) arising from A_1 and inserting onto the medial face of the maxilla is also primitively present, although usually only weakly developed. Within the Labroidei (and some percoids), there is no association of A_1 with the maxillo-mandibular ligament and maxillary control is primarily through tA_1 (Stiassny, 1980, 1981). The relative insertion sites of tA_1 in cichlids, embiotocids and labrids have been suggested to represent a morphocline of insertion from just below the cranial condyle (cichlids, Fig. 18C), to well onto the cranial condyle (in some embiotocids, Fig. 18A), to a point at the anterior margin of an elongate cranial condoyle (labrids, Fig. 18D). The insertion of tA_1 onto the cranial condyle was considered by Stiassny (1980) to be a synapomorphy of an embiotocid-labrid clade. Further investigation of this feature indicates that in fact this character exhibits a continuous range of variation both within and between taxa examined. For example, the embiotocids span a range of tA_1 insertions (Figs. 18A, B) from that found in cichlids and many other percoids to a condition approaching that of labrids. Within the Cichlidae, in addition, one occasionally finds a condition approaching that of the Labridae (e.g., in the etropline Cichlidae). In view of this, we feel that we would be creating an artificial discontinuity in what is in fact a continuous range of variation if we regarded tA_1 insertion as a synapomorphy of the Embiotocidae and Labridae.

Character Analysis

Figure 19 depicts the single minimum length tree derived by the PAUP branch and bound routine (Swofford, 1985). This is the shortest tree obtained from the character data (length = 23, consistency index = 0.652) and we favor it with due reservation. The resultant scheme of relationships differs from others previously proposed by Stiassny (1980), Liem and Greenwood (1981), and most recently by Kaufman and Liem (1982), in placing the Cichlidae as the sistergroup of all the remaining labroid groups. The integrity of a monophyletic assemblage composed of the Embiotocidae, Pomacentridae, and Labridae is supported by the presence of three uniquely derived features of the pharynx: the fifth ceratobranchial elements forming the LPJ are completely united such that no trace of a median suture remains, and the pharyngeal tooth rows span radially across the LPJ and overlie the median portion of the jaw (character 1 in Fig. 19); the urohyal articulates via its dorsal process with the first basibranchial element (character 2 in Fig. 19); and the musculus cranio-pharyngobranchialis 2 is absent (character 3 in Fig. 19). The Embiotocidae is placed as the sistergroup of the Pomacentridae plus the Labridae, again in contrast to previous hypotheses of other authors. Four pomacentrid/labrid synapomorphies are identified in a range of structural systems (characters 4, 5, 6, and 7 in Fig. 19).

Although Figure 19 represents the most

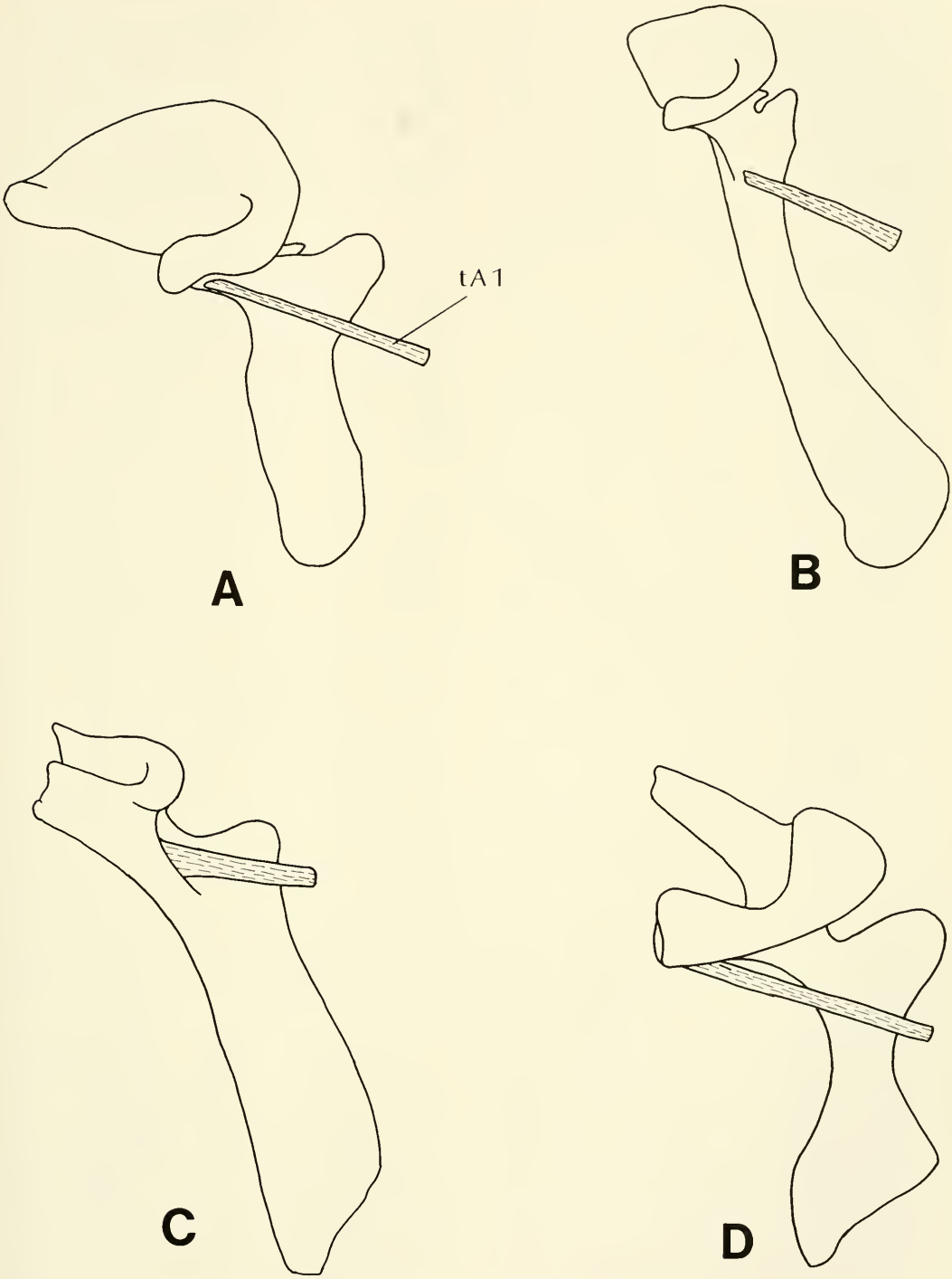


Figure 18. Insertion of tA_1 into the maxilla in: A. *Embiotoca*; B. *Hyperprosopon*; C. *Cichla*; D. *Labrus*.

parsimonious interpretation of the data at hand, the number of crossbars superimposed onto the cladogram starkly illustrates that even this scheme requires the loss or independent gain of many derived characters. Specifically, our hypothesis requires either that the Embiotocidae and Labridae have independently lost the second pharyngeal toothplates and reduced the pharyngobranchial element to a small rod-like structure (character 8), lost the interarcual cartilage (character 10), and have independently reduced (Embiotocidae) and lost (Labridae) the fourth upper toothplate (character 9), or alternatively that the Pomacentridae has undergone a reversal in each of these features. The Cichlidae and Labridae would have to have independently reduced the number of caudal epurals (character 11), reduced the number of predorsals (character 12), and developed an endopterygoid shelf with an (associated) shift in adductor arcus palatini muscle insertion site (character 13). The pomacentrids and embiotocids would have to have independently fused the second extrascapular bone with the parietal (character 14), or alternatively the Labridae would have to have secondarily reexpressed the ancestral condition of this character. Finally, the Pomacentridae would have to have redeveloped an autogenous antepenultimate hemal spine (character 15).

Obviously when dealing with such large amounts of homoplasy a number of alternative trees of nearly equivalent length can be computed. Figure 20 depicts all of the trees derived from our character data that are of length 27 or less. There is one tree of length 24 (1a in Fig. 20) and this, like our favored tree depicted in Figure 19, also places the Cichlidae as the sistergroup of the remaining Labroidei. Thus, the two shortest trees computed correspond in their placement of the Cichlidae, but differ as to which clade, the Embiotocidae or the Pomacentridae, forms the sistergroup of the Labridae. No trees of length 25 can be derived from these data. Diagrams 2a–f and 3a–b (Fig. 20) represent trees of lengths 26 and 27 respectively. Of the trees represented in Figure 20, only 2a has been previously proposed as a labroid phylogeny (Kaufman and Liem, 1982; Stiassny, 1980). There are two trees of length 29, including the tree of Liem and Greenwood (1981), and two trees of length 30.

Given the plethora of possible trees of nearly equivalent length and yet widely varying topologies, it is clear that statements of relationship within the Labroidei must remain highly tentative. For this reason it would be ill-advised to propose any classificatory or nomenclatural changes based upon the results of our study. Perhaps the most significant observation we can make is that morphological character transformations within the Labroidei display a disconcertingly large amount of homoplasy. No matter which scheme of relationship is ultimately chosen, we must accept and acknowledge that in many structurally (and functionally?) disparate systems, character distributions within the Labroidei present a perplexing "web of parallelism." As systematic morphologists we are obviously interested in knowing whether the degree of homoplasy revealed in our study of the Labroidei is a general phenomenon that will be observed repeatedly in different groups that are subject to such detailed morphological analysis, or if the magnitude of the problem is peculiar to this group—and is therefore perhaps indicative of something particular about its morphological evolution.

We hope that future work incorporating other types of data, for example cladistically analysed physiological or biochemical data (Wiley, 1981), will provide a set of characters more clearly supporting a single phylogeny. Once such a single, highly corroborated phylogeny is available, then the same morphological homoplasy that proved an impediment to our understanding of the relationships of the group suddenly becomes of great poten-

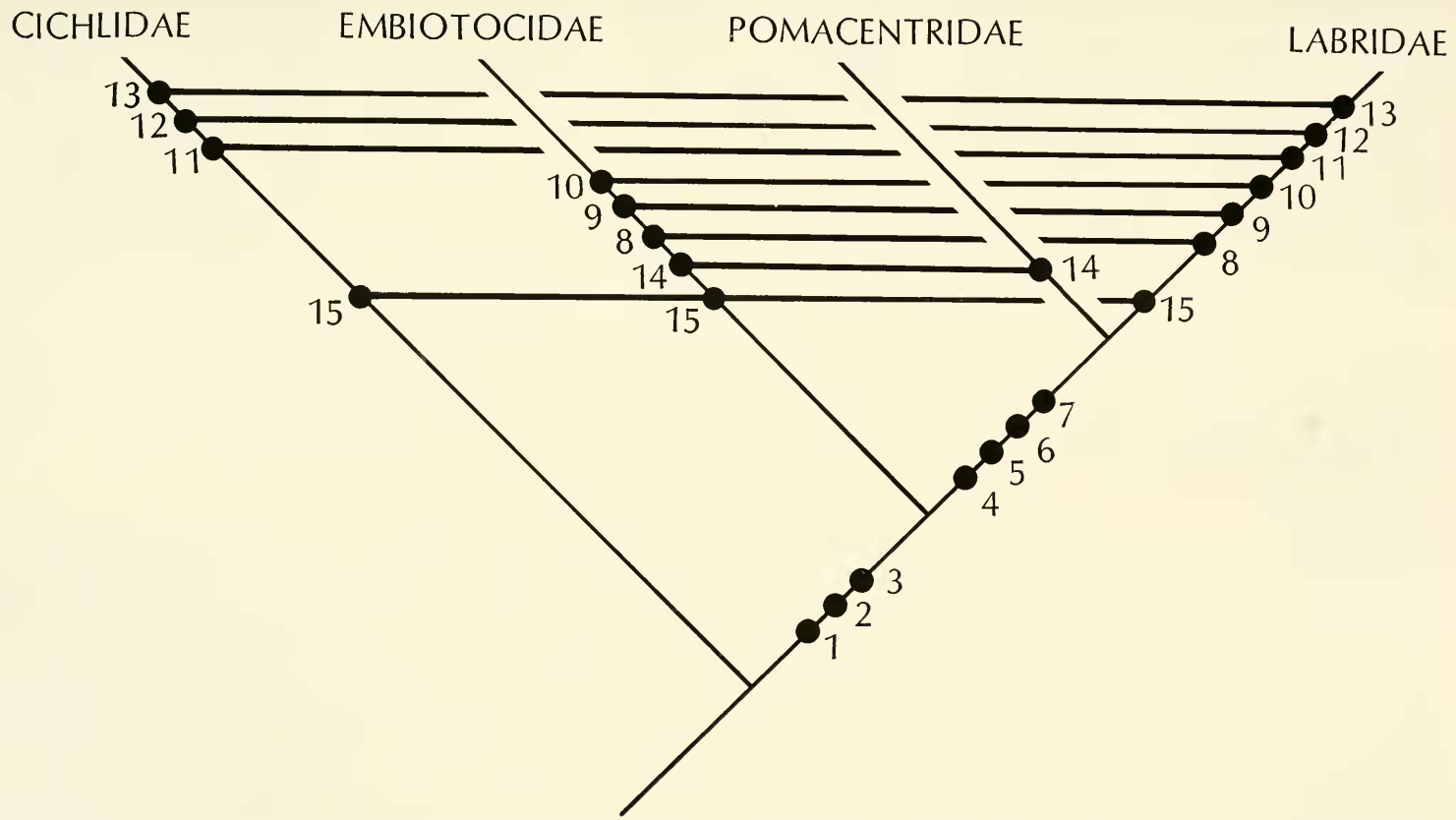


Figure 19. Cladogram of labroid relationships proposed in this study. Characters are: 1. LPJ with no trace of a central suture, and with pharyngeal teeth implanted directly over the midline. 2. Urohyal articulates with basibranchial one. 3. M. cranio-pharyngobranchialis 2 division of the transversus dorsalis muscle absent. 4. LPJ "Y-shaped" with short body and elongate lateral horns. 5. Obliquus ventralis IV and rectus ventralis V insert separately onto the semicircular ligament system. 6. Basibranchial one bears a large keel-like ventral extension. 7. Uroneural fused with the urostyle. 8. Second pharyngobranchial toothplate absent. 9. Fourth upper toothplate either markedly reduced or entirely lacking. 10. Interarcual cartilage absent. 11. Reduced number of caudal epurals. 12. Two of fewer predorsal bones. 13. Endopterygoid shelf absent and adductor arcus palatini inserts onto medial face of the suspensorium. 14. Extrascapular bone fused to the parietal. 15. Hemal arch of the antepenultimate caudal vertebra fused with the centrum.

tial use in extending our understanding of its evolution. Clades such as the Labroidei will provide an ideal opportunity for developmental genetecists, physiologists and morphologists to explore and elucidate the causal processes underlying morphological homoplasy.

DISCUSSION

Pharyngeal Complexity and Systematic Dominance

Of the eight characters found to diagnose the Labroidei, seven are elements of the PJA, and the eighth, although not obviously linked with the functioning of that apparatus, is a feature of the pharynx. Despite a conscious effort to locate additional synapomorphies in other structural systems we were able to find evidence of labroid monophyly only in the pharynx.

This predominance of PJA characters has not extended to our analysis of relationships within the Labroidei. Although features of the pharynx are well represented among the characters used, enough other characters from a reasonable "spread" of morphological systems are introduced so that pharyngeal information is not overwhelming at that level of analysis. Of the 15 characters used in the analysis of labroid intrarelationships (Figs. 19 and 20) only six are components of the PJA (characters 1, 3, 4, 8, 9 and 10). Three additional characters are located in the pharyngeal region but have no obvious functional connection with the PJA (characters 2, 5 and 6), and the remainder are distributed throughout the organism (characters 7, 11, 12, 13, 14 and 15). Despite the variety of sources of information regarding relationships within the Labroidei, we feel that the predominance of the pharynx as a source of information at the subordinal level is noteworthy and credits further consideration here.

When a particular morphological structure or functional complex plays such a disproportionately predominant role in the systematics of a group of organisms there are several reasons why that region or complex may be of interest. While freely acknowledging that many non-morphological features can be of equal, and sometimes even primary, importance in the evolution of groups and their interrelationships (Mayr, 1969; Miller, 1949), we will restrict ourselves to a consideration of the particular morphological properties of groups:

1. The skewed emphasis may reflect an historical bias in the taxonomy of the group. For example, "caudal characters" may have traditionally (originally) been used in analyses and subsequent workers have followed the precedent and directed attention to the complex.
2. For some reason a particular region/character complex may be assessed a priori to be of no significance in the evolution of the group, and thus attention has been centered upon the region. This emphasis reflects what Mayr (1969) has termed the "Darwin Principle" in systematics and stresses the use of conservative, "non-functional/non-adaptive" characters in systematic analyses.
3. For some reason a particular region/character complex may be assessed a priori to be of particular significance in the evolution of the group, and thus attention has centered upon the region. This is the opposite position to the preceding case, and emphasizes the use of malleable "functional/adaptive" characters. Although few authors are explicit in their formulation of this approach it is implicit in the works of a number of functional morphologists (e.g., Dullemeijer, 1974; Gutmann, 1977) and "evolutionary" taxonomists (e.g., Szalay, 1981; see also discussion in Cracraft, 1981a).

Each of the above can loosely be viewed as resulting in some sort of taxonomically introduced bias, and subsequent investigation of other morphological complexes would render a range of additional characters for analysis and

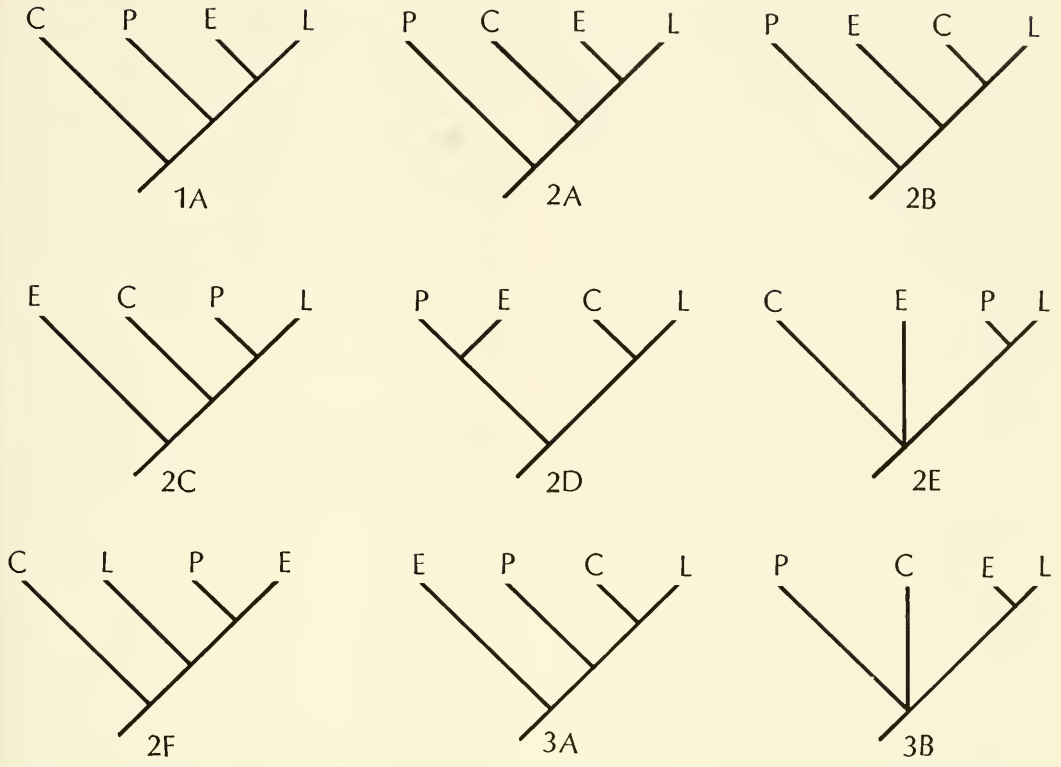


Figure 20. Range of additional trees (of length 27 or less) derivable from the character data entered into the analysis. 1A (length 24), 2A–F (length 26), and 3A–B (length 27). C = Cichlidae, P = Pomacentridae, E = Embiotocidae and L = Labridae.

the predominance of the original complex may be expected to be reduced. This isn't, of course, to say that those original features suddenly become unimportant or insignificant, but only that they no longer predominate.

In view of our conscious effort to locate features other than pharyngeal ones uniting the Labroidei and our inability to find any, we suggest that it is improbable that investigator bias is responsible for the importance of the pharynx in diagnosing the clade. Of course we cannot rule out the possibility that other morphological information does exist and that we have simply not found it yet, but our hypothesis is that such data do not exist.

4. Predominance of the region may simply be a reflection of structural (and/or functional) complexity. As Lauder (1981) quite correctly pointed out, few morphologists have explicitly considered the influence of complexity upon patterns of morphological change. Intuitively at least, it seems that complex systems have a higher likelihood of change than simple ones. If complexity is defined as the number of parameters needed to describe form (Lauder, 1981; Vermeij, 1973), then an increase of complexity will automatically increase the number of possibilities for change in the component elements and in their relations to one another. Complex systems have more potentially stable intermediate states and have, therefore, options for change in design at each level (Lauder, 1981; Simon, 1962).

The euteleostean pharynx is a highly complex construction, composed of many elements and numerous struc-

tural and functional networks of interconnection. Lauder (1983) showed that there is a degree of decoupling between patterns of functional activity and the sequence of structural modification in the euteleostean pharynx. In this complex system overall functioning can be maintained in the face of sequential structural modification. In view of the complexity of the system, and concomitant structural variation, it is perhaps not surprising that so much attention has been centered upon pharyngeal characters in the systematics of euteleostean clades (e.g., Nelson, 1969; Rosen, 1973; Rosen and Parenti, 1981).

We doubt whether a case can be made that the labroid pharynx is more complex than that of other clades; complexity alone does not seem to account for our observation of pharyngeal dominance in labroid systematics.

5. The predominance of any particular region/character complex may indicate that it actually represents some significant and independent locus of evolutionary change.

With all of the caution that the preceding list engenders, we would nonetheless like to speculate that our findings may indicate that the PJA does indeed represent precisely this sort of major locus of evolutionary change for the labroid clade. That features of the pharynx alone seem to characterize the Labroidei indicates that, relative to other systems, this complex underwent extensive restructuring early in the history of the clade. Perhaps, as suggested by Liem (1973), a single change in one aspect of this complex precipitated a major restructuring in other elements of the pharyngeal network. Initial restructuring of the pharynx, a complex considered to be profoundly important in the evolution of the Labroidei (see discussion of the concept of key innovation below), may then have been a very rapid, yet integrated, event.

If this is the case, the pharynx may easily be overemphasized as a source of *systematic* information since many of the characters treated as independent (and equivalent) are a necessary result of the single initial change. The remarkable mirroring of a whole suite of morphological features of the PJA in the phylogenetically disparate labroids and beloniforms would appear to support this inference. Recognition of what constitutes a "unit-character" in a situation such as this is obviously fraught with difficulty.

Key Innovations and the Explanation of Differential Diversity

According to recent studies, features of the pharynx may have had important consequences for the morphologic and taxic diversity of the Labroidei (e.g., Lauder, 1983; Liem, 1973, 1980; Liem and Osse, 1975; Liem and Sanderson, 1986). Early suggestions that the acquisition of a novel structure (e.g., an LPJ suspended by a muscle sling) could profoundly influence the subsequent evolution of a lineage usually involved the idea of the novel feature allowing entry into a new adaptive zone (e.g., Mayr, 1963; Simpson, 1944, 1953, 1959).

Subsequent radiation in an arena of reduced competition gave rise to diverse and/or speciose lineages, the success of which could then be attributed to the acquisition of the unique feature characterizing them. The importance of such an "adaptive breakthrough" in transpecific evolution and the origin of higher taxa has been repeatedly stressed in subsequent explanations of organismic diversity (and enhanced speciation?) (e.g., Jaanusson, 1981; Liem, 1973, 1980; Miller, 1949; Stanley, 1968). A plethora of names for this "distinctive sort of adaptation" (Simpson, 1953) is available (e.g., key adjustments, key inventions, key evolutionary novelties, major adaptive innovations). For ease of discussion we will follow Lauder (1981) in adopting the term key innovation (KI).

Most recently, in a pair of perceptive

and insightful publications Lauder (1981, 1982a) critically analyzed the key innovation concept. His primary criticism, with which we concur, is that a hypothesis that a structure plays a "key" (causal?) role in the subsequent evolution of a lineage is untestable within the framework usually proposed. If an evolutionary novelty is indeed unique, how can any hypothesis regarding its importance be tested by comparison with its influence in independent circumstances? Unique events do not allow a critical analysis of their consequences.

As a solution to this dilemma, Lauder (1981, 1982a) suggested that general attributes (emergent organizational properties) of unique features be sought, so that the consequences of these general features can be compared in both closely related and distantly related taxa. In this sense, it is not only the particular physical features located in compared taxa that are the putative KIs but also the general or emergent properties resulting from them. Lauder provided us with a method to bypass the evolutionary "uniqueness" of specific morphologies by concentrating attention on general, and thus comparable, properties. As an example of such a general property, Lauder (1981) discussed the decoupling of primitively constrained systems and its possible consequences on the subsequent evolution of a taxon. Precisely such a functional decoupling between buccal and pharyngeal jaws, following key innovational pharyngeal specialization, is proposed to have played a central role in the extensive trophic diversification of cichlid fishes (Liem, 1973; Liem and Osse, 1975). The development of a highly integrated PJA (later found to characterize the Labroidei as a whole, see pages 273–288), and the subsequent freeing of the buccal jaws from a major role in food preparation prior to deglutition (Liem's second major function), is held to have resulted in an extreme specialization of the buccal apparatus.". . .The release of the restricting influence of the second major function resulted in the emergence of numerous specializations of collecting mechanisms dealing with dramatically diverse foods." (Liem, 1973: 41). The resultant ability of the clade to exploit a great variety of trophic resources is considered to be of central importance in cichlid trophic diversification, ecological predominance, and explosive speciation (e.g., Fryer and Iles, 1972; Greenwood, 1974, 1984; Liem, 1973, 1980). If this particular PJA configuration was indeed an unique evolutionary novelty then no comparison of its effects in other clades would be possible and its consequences could not be assessed (but see discussion of the beloniform parallel on pages 310–312). However, as decoupling is a general or emergent property transcending the features of any particular system, one can legitimately look elsewhere for clades that exhibit comparable structural and/or functional decoupling. A relationship between decoupling and, for example, morphological diversity between terminal taxa of both clades can now be sought. Following Lauder (1981, 1982a; Liem and Wake, 1985), one may pose the relational hypothesis that the emergence of a general property (Z in Fig. 21A) has consequences for the diversity of terminal taxa (A–D in Fig. 21A). The proposed method of testing this hypothesis is the repeated assessment of diversity (or whatever parameter is being judged) within and between unrelated lineages also possessing this general property (Z′ and Z″, Fig. 21A). If no relationship between the presence of this property and a particular pattern is found, the hypothesis is rejected.

However, if such a comparative test is to be meaningful, one cannot directly compare attributes of the taxa in which the putative KIs occur. Diversity (like species richness) is a relative term and if a clade or set of clades is to be considered diverse (or speciose), this determination can only be made with respect to some meaningful standard of comparison. A consideration of the phylogenetic context of each taxon provides the only meaning-

ful standard for comparison. As is implicit in Hennig (1966: 225) and Lauder (1981, 1982a), it is the sistergroup of the taxon possessing the putative KI that provides the standard by which diversity (or species richness) may be judged (see also excellent discussion in Cracraft, 1981b, 1982).

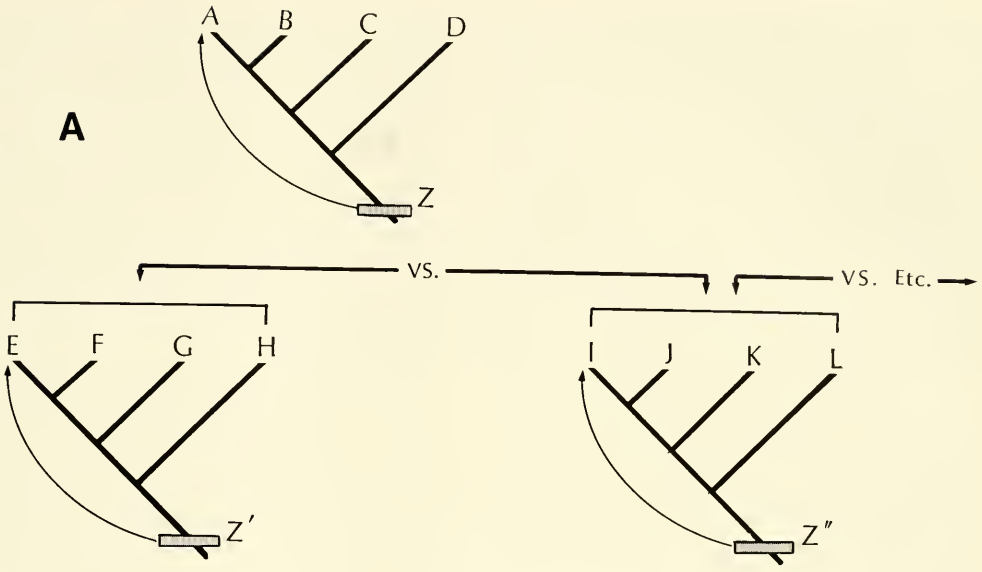
We would like to emphasize the need for comparison between the clade possessing the putative KI and its sistergroup lacking it (A–D/X in Fig. 21B) in assessments of diversity or species richness. Accordingly comparisons of species number (or diversity) are made between clades that have equivalent histories up to the time of their divergence. They are of equal age, began with equivalent developmental programs, and differ only in those features arising (or re-emerging) after their divergence. In these important features then, the sistergroup is the closest approximation we have to what the lineage under consideration would be like had it not developed the KI (and other evolutionary novelties characterizing it). As illustrated by Figure 21B, testing of hypotheses regarding the role of a key innovation becomes a two step process. Step one (Fig. 21B) provides a measure of the relative diversity of the taxon possessing the putative KI (A–D in Fig. 21B) and its sister group (X in Fig. 21B). In the second step (step 2 in Fig. 21B) relative diversities are then compared *between* independent lineages in which comparable key innovations have arisen (Step 2 in Fig. 21B: E–H to X′ versus I–L to X″). In this way possibly confounding historical factors are held to a minimum and the relative nature of the term diversity (or species richness) is acknowledged and, as far as is possible, is accounted for (but see discussion on pages 312–313).

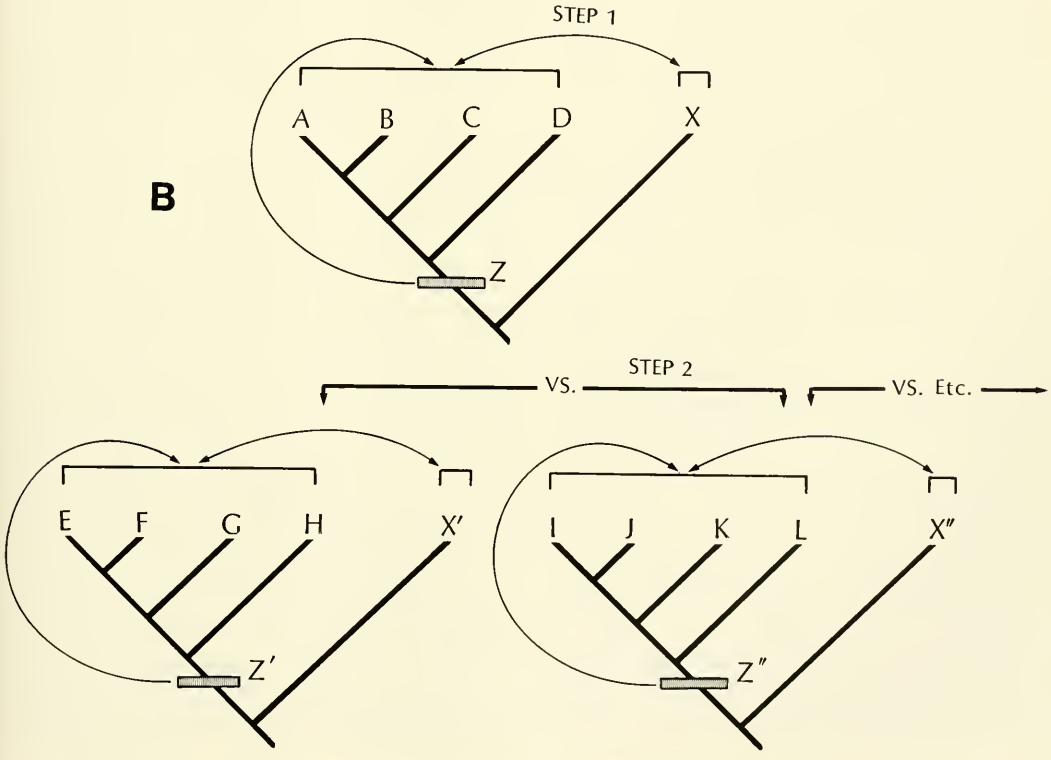
In past considerations of the key innovation concept it is frequently unclear what exactly the concept is meant to explain. A key innovation is frequently invoked to account for the success of a lineage, but many properties might be used to characterize a particular lineage as successful. For example, enhanced speciation rates, reduced extinction rates, or morphological diversification are all perfectly reasonable criteria of particular kinds of success. In discussions or hypotheses of a key innovation, species richness and morphological diversity are often used interchangeably or treated as if they are so closely related as to render distinction unnecessary. While it may frequently be the case that morphological differentiation is the by-product of the speciation process, it is by no means necessarily so, as is evidenced by the well-documented phenomenon of sibling species (Mayr, 1976; McKaye *et al.*, 1982). Nor is it necessarily the case that morphological diversity within a lineage can be explained simply as the sum of differentiations accompanying speciation (Simpson, 1944, 1953). Even if morphological diversity is the proposed outcome of the origin of a key innovation, it must also be clearly specified what types of features are in fact diversifying. Is it the specific morphological complex involving the key innovation or the organism as a whole that is supposed to undergo change? Any test of the effect of structural features or their emergent properties on the evolution of a lineage will require an explicit prediction of the nature of the consequences of their presence.

The need to precisely specify the nature of the predicted consequences of a key innovation is clearly evident when we consider the development of a pharyngeal muscle sling and Liem's (1973) hypothesis of its effect on subsequent evolution. As described on pages 274–266, within the Beloniformes, one finds a striking morphological parallel between the configu-

→

Figure 21. Testing of relational hypotheses involving correlations between the possession of emergent features (Z) and the resultant properties of groups. A. After Lauder (1981); B. Test incorporating initial intracladal sistergroup (X) comparison (step 1) prior to intercladal comparison (step 2). (see page 310 for further explanation of figure).


A
A
B
C
D
Z
VS.
VS. Etc.
E
F
G
H
Z′
I
J
K
L
Z″


B
STEP 1
A
B
C
D
X
Z
STEP 2
VS.
VS. Etc.
E
F
G
H
X′
Z′
I
J
K
L
X″
Z″

ration of the PJA of labroids (Fig. 6) and that of the Exocoetoidea (Fig. 2). In these fishes (the Hemiramphidae and Exocoetidae) the fourth levator externus muscle (and a portion of the levator posterior) form a muscle sling supporting the fused fifth ceratobranchial elements. In addition, the dorsal musculature (particularly the transversus dorsalis posterior) is reduced and the articulatory facets of the third pharyngobranchials are exposed to form a diarthrosis with a well-developed neurocranial apophysis (Fig. 2E). The Scomberescoidea lack these features although, like the Exocoetoidea, they possess a completely united LPJ in which no trace of a median suture is evident. The LPJ also bears a well-developed median keel onto which the transversus ventralis muscle inserts.

The fortuitous morphological mirroring of aspects of the labroid PJA by that of non-adrianichthyoid beloniforms allows at least one test of the evolutionary consequences of a putative key innovation in these phylogenetically disparate assemblages. However, for this test to be unambiguous we need a clearly stated hypothesis of the consequences of the key innovation. For example, if our prediction is increased species number, we find that the Exocoetoidea is indeed more successful than its sister lineage, the Scomberesocoidea (Fig. 7; 135+ species in the Exocoetoidea versus 36 species in the Scomberesocoidea, Nelson, 1984). This would seem to support the hypothesis of this particular pharyngeal configuration being key to the taxic success of a lineage. Likewise, if diversity of the trophic apparatus as a whole is the predicted outcome, then the wide range of tooth morphologies of both the PJA and the buccal jaws found in the Exocoetoidea relative to the Scomberesocoidea (Collette, 1966, 1974, 1976; Parin, 1961) would lend support to this hypothesis. However, the Scomberesocoidea exhibits a far greater diversity of LPJ form (but not dentition) than does its sister lineage (e.g., compare figs. 2, 3 of Collette, 1966 with fig. 16 of Parin, 1961). In this respect, the Exocoetoidea can be considered to lack significant diversity, indicating that the development of a muscle sling has not resulted in an overall pharyngeal diversification. Thus it would seem that clarification and explicit statement of the proposed consequences of the development of the key innovation are a necessary prerequisite for the generation of hypotheses about generality of effects and the role of KIs in evolution.

Despite the methodological refinement of Lauder's scheme outlined here (Fig. 21B), rigorous testing of historical hypotheses still presents difficulties. Even given a reasonable number of independent clades in which to conduct comparisons, it seems unlikely that comparisons of lineages sharing a putative KI with their respective sistergroups (the first step in our analysis) will always lead to unambiguous statements regarding the role of those innovations in, for example, cladogenesis. If our hypothesis is that the presence of a key innovation is somehow implicated in enhanced speciation rates (or morphological diversification), this would be refuted by finding a clade with a comparable key innovation which is depauperate relative to its sistergroup. However, the question immediately arises as to how comparable these sister lineages are with respect to the suite of extrinsic factors acting upon them after their origin (see also Cracraft, 1982). Any differences in species richness or morphological diversity found in the two clades might as easily be the result of differences in their habitat (e.g., estuary versus coral reef), vicariant history (e.g., mid-ocean versus shallow lake basin), later behavioral developments, and so on. Almost inevitably there will be many ways in which the factors affecting species richness or diversity will differ due to the independent histories of sister lineages subsequent to their phylogenetic origin.

Likewise, the second phase of the analysis (i.e., comparison of independent clades

within which the key innovation arises; step 2 in Fig. 21B) presents its own difficulties. It might not be the case that the same evolutionary "novelty" or property will have equivalent effects when arising in different phylogenetic contexts. How likely is it that two different lineages, each with its own intrinsic morphological constraints, developmental pattern, etc. will respond in the same way to the appearance of the "same" evolutionary novelty or property? While each appearance of the evolutionary novelty would indeed be independent, it might not be comparable because the innovation would, in each case, appear against a unique historical background, a set of existing functional constraints, and would be subject in the course of subsequent evolution to a unique set of extrinsic factors. The consequences of, for example, decoupling in one component of the trophic apparatus (e.g., the buccal jaws) may be very different, depending on the limitations imposed by primitive constraints on other components of the trophic apparatus (e.g., pharyngeal jaws). While the first step of the analysis would not be affected, since the network of constraints would be primitive for both taxa (A–D *and* X; Fig. 21B), the nature of the constraints affecting independent taxa (E–H to X′ vs. I–L to X″; Fig. 21B) might differ greatly and thus have different interactions with the putative key innovation. Even if an innovation may be implicated in cladogenesis (e.g., Stanley, 1975) or diversification in one case, in another case it might arise in a context in which pre-existing functional networks or subsequent environmental influences are so constraining as to overwhelm its role in diversification or cladogenesis. Thus, assertions about the influence of key innovations, even when situated in a strictly phylogenetic framework, run the risk of being reduced to particularistic explanations about unique events in an unique historical arena.

Despite the problems alluded to above, we concur with Lauder (1982b: 66) that "The key to discovering the limits to deterministic explanation in the historical record will be the extent to which general historical pathways in the transformation of biological design are revealed by a phylogenetic analysis of structural and functional patterns." The structural approach to historical patterns advocated by Lauder renders phylogeneticists with a method with which to begin that search. Discovery of such general historical pathways will have profound implications regarding the nature of the evolutionary process.

ACKNOWLEDGMENTS

We would like to thank the following individuals and institutions for the loan of material and/or helpful information and comments: Karel F. Liem, Karsten E. Hartel, Peter Karlsberg, and Robert J. O'-Hara (Museum of Comparative Zoology, Harvard University), the members and visitors to our departmental "Fish Group" (Department of Organismic and Evolutionary Biology, Harvard University), William F. Smith-Vaniz (Academy of Natural Sciences, Philadelphia), Victor G. Springer and Richard P. Vari (National Museum of Natural History, Washington), and Leslie S. Kaufman (New England Aquarium, Boston). The Friday Harbor Marine Laboratory, University of Washington, generously provided hospitality and support to J.S.J. during early stages of this work. We particularly thank Ward Wheeler, Wayne Maddison, and David Maddison who were so generous with their computer programs and expertise. Finally, for their thorough and critical review of the manuscript, we are grateful to Stanley H. Weitzman and G. David Johnson (National Museum of Natural History, Washington), and an additional anonymous reviewer; their thoughtful input is much appreciated.

Much of the impetus behind this paper stems from our reading of a manuscript circulated for comment by the late Donn E. Rosen. As with all of Donn's work, that manuscript was stimulating and thought

provoking, and it is with a profound sense of gratitude and loss that we dedicate this paper in his memory.

Financial support for this research was provided by a National Science Foundation Grant (No. BSR 84-07449) to M.L.J.S. and a National Science Foundation Graduate Fellowship to J.S.J. Publication costs of this study were covered in part by a grant from the Wetmore Colles Fund.

LITERATURE CITED

AERTS, P. 1982. Development of the musculus levator externus 1V and the musculus obliquus posterior in *Haplochromis elegans* Trewavas, 1933 (Teleostei: Cichlidae): A discussion on the shift hypothesis. Journal of Morphology, **173:** 225–235.

ANKER, G. CH. 1978. The morphology of the head muscles of a generalized *Haplochromis* species: *H. elegans* Trewavas, 1933 (Pisces, Cichlidae). Netherlands Journal of Zoology, **28:** 234–271.

BARLOW, G. W., AND J. W. MUNSEY. 1976. The Red Devil-Midas-Arrow cichlid species complex in Nicaragua, pp. 359–369. *In* T. B. Thorson (ed.), Investigations of the Ichthyofauna of Nicaraguan Lakes. Lincoln, Nebraska: School of Life Sciences, University of Nebraska. x + 663 pp.

BAREL, C. D. N., F. WITTE, AND M. J. P. VAN OIJEN. 1976. The shape of the skeletal elements in the head of a generalized *Haplochromis* species: *H. elegans* Trewavas 1933 (Pisces, Cichlidae). Netherlands Journal of Zoology, **26:** 163–265.

BERG, L. S. 1940. Classification of fishes and fish-like vertebrates, living and fossil. Russian and English lithoprint, **1947:** 87–517. Ann Arbor, Michigan.

BERTIN, L., AND C. ARAMBOURG. 1958. Superordre des Teleosteens, pp. 2204–2500. *In* P. Grasse (ed.), Traite de Zoologie, Anatomie, Systematique, Biologie. Volume 13 Agnathes et Poissons. Paris: Grassé.

BRETT, J. R. 1979. Some morphological and behavioural adaptations of the pile perch (*Rhacochilus vacca*) feeding on mussels (*Mytilus edulis*). Canadian Journal of Zoology, **57:** 658–664.

CLAEYS, H., AND P. AERTS. 1984. Note on the compound lower pharyngeal jaw operators in *Astatotilapia elegans* (Trewavas), 1933 (Teleostei: Cichlidae). Netherlands Journal of Zoology, **34:** 210–214.

COLLETTE, B. B. 1966. *Belonion*, a new genus of fresh-water needlefishes from South America. American Museum Novitates, **2274:** 1–22.

———. 1974. South American freshwater needlefishes (Belonidae) of the genus *Pseudotylosaurus*. Zoologische Mededelingen. Leiden, **48**(16): 169–186.

———. 1976. Indo-West Pacific halfbeaks (Hemiramphidae) of the genus *Rhynchorhamphus* with descriptions of two new species. Bulletin of Marine Science, **26**(1): 72–98.

COLLETTE, B. B., G. E. GOWEN, N. V. PARIN, AND S. MITO. 1984. Beloniformes: Development and relationships, pp. 335–354. *In* H. G. Moser (ed.-in-chief), Ontogeny and Systematics of Fishes. Special Publications of the American Society of Ichthyologists and Herpetologists No. 1. Lawrence, KS: Allen Press. 760 pp.

CRACRAFT, J. 1981a. The use of functional and adaptive criteria in phylogenetic systematics. American Zoologist, **21:** 21–36.

———. 1981b. Pattern and process in paleobiology: the role of cladistic analysis in systematic paleontology. Paleobiology, **7**(4): 456–468.

———. 1982. A non-equilibrium theory for the rate control of speciation and extinction and the origin of macroevolutionary patterns. Systematic Zoology, **31**(4): 348–365.

DE MARTINI, E. E. 1969. A correlative study of the ecology and comparative feeding mechanism morphology of the Embiotocidae (surf-fishes), as evidence of the family's adaptive radiation into available ecological niches. The Wasmann Journal of Biology, **27**(2): 117–247.

DIETZ, P. A. 1921. Beitrage zur Kenntnis der Keifer- und Kiemengogenmuskelatur der Teleosteir. Mitteilungen aus der Zoologischen Station zu Neapel. Berlin, **22**(13–16): 433–457.

DINGERKUS, G., AND L. D. UHLER. 1977. Enzyme clearing of Alcian Blue stained whole small vertebrates for demonstration of cartilage. Stain Technology, **52**(4): 229–232.

DULLEMEIJER, P. 1974. Concepts and Approaches in Animal Morphology. Assen, The Netherlands: Van Gorcum. xii + 270 pp.

———. 1980. Functional morphology and evolutionary biology. Acta Biotheoretica, **28:** 151–250.

DULLEMEIJER, P., AND C. D. N. BAREL. 1977. Functional morphology and evolution. *In* M. K. Hecht, P. C. Goody, and B. M. Hecht (eds.), Major Patterns in Vertebrate Evolution. London: Plenum Press. ix + 908 pp.

ELDREDGE, N., AND J. CRACRAFT. 1980. Phylogenetic Patterns and the Evolutionary Process. Methods and Theory in Comparative Biology. New York: Columbia University Press. 349 pp.

EMERY, A. R. 1973. Comparative ecology and functional osteology of fourteen species of damselfish (Pisces: Pomacentridae) at Alligator Reef, Florida Keys. Bulletin of Marine Science, **23**(3): 649–770.

FARRIS, J. S. 1972. Estimating phylogenetic trees from distance matrices. American Naturalist, **106:** 645–668.

FORD, E. 1937. Vertebral variation in teleostean fishes. Journal of the Marine Biological Society of the United Kingdom. Plymouth, **22:** 1–37. Figs. 1–18, Pls. 1–16.

FRYER, G., AND T. D. ILES. 1972. The Cichlid Fishes of the Great Lakes of Africa. Their Biology

and Evolution. Edinburgh: Oliver and Boyd. 641 pp.

FUTUYMA, D. J. 1979. Evolutionary Biology. Greenfield, Mass.: Sinauer Associates, Inc. x + 565 pp.

GOBALET, K. W. 1980. Functional morphology of the head of parrotfishes of the genus *Scarus*. Ph.D. thesis, University of California at Davis.

GOEDEL, W. VON 1974a. Beitrage zur vergleichenden und funktionellen Anatomie des Kopfes von *Tilapia* (Cichlidae, Teleostei). Teil. 1 Zoologische Jahrbuecher Anatomie, **92:** 220–274.

———. 1974b. Beitrage zur vergleichenden und funktionellen Anatomie des Kopfes von *Tilapia* (Cichlidae, Teleostei). Teil. 2 Zoologische Jahrbuecher Anatomie, **92:** 321–383.

GOMON, M. F., AND J. P. PAXTON. 1986. A revision of the Odacidae, a temperate Australian-New Zealand labrid family. Indo-Pacific Fishes, **8:** 1–57.

GOSLINE, W. A. 1961. The perciform caudal skeleton. Copeia, **1961**(3): 265–270.

———. 1966. The limits of the fish family Serranidae, with notes on other lower percoids. Proceedings of the California Academy of Sciences, **33**(6): 91–112.

GREENWOOD, P. H. 1974. Cichlid fishes of Lake Victoria, east Africa: the biology and evolution of a species flock. Bulletin of the British Museum of Natural History (Zoology) supplement, **6:** 1–134.

———. 1978. A review of the pharyngeal apophysis and its significance in the classification of African cichlid fishes. Bulletin of the British Museum of Natural History (Zoology), **33:** 297–323.

———. 1984. African cichlids and evolutionary theories, pp. 141–154. *In* A. A. Echelle and I. Kornfield (eds.), Evolution of Fish Species Flocks. Orono, Maine: University of Maine at Orono Press. 257 pp.

———. 1985. Notes on the anatomy and phyletic relationships of *Hemichromis* Peters, 1858. Bulletin of the British Museum of Natural History (Zoology), **48:** 131–171.

GREENWOOD, P. H., D. E. ROSEN, S. H. WEITZMAN, AND G. S. MYERS. 1966. Phyletic studies of teleostean fishes, with a provisional classification of living forms. Bulletin of the American Museum of Natural History, **131:** 339–455.

GUNTHER, A. 1880. An Introduction to the Study of Fishes. Edinburgh: Adam and Charles Black. xvi + 720 pp.

GUTMANN, W. F. 1977. Phylogenetic reconstruction: theory, methodology, and application to chordate evolution, pp. 645–669. *In* M. K. Hecht, P. C. Goody, and B. M. Hecht (eds.), Major Patterns in Vertebrate Evolution. London: Plenum Press. ix + 908 pp.

HENNIG, W. 1966. Phylogenetic Systematics. Urbana: University of Illinois Press. 263 pp.

HIXON, M. A. 1980. Competitive interactions between California reef fishes of the genus *Embiotoca*. Ecology, **61**(4): 918–931.

HOLLISTER, G. 1936. Caudal skeleton of Bermuda shallow water fishes. I. Order Isospondyli: Elopidae, Megalopidae, Albulidae, Clupeidae, Dussumieriidae, Engraulidae. Zoologica, **21:** 257–290.

———. 1937. Caudal skeleton of Bermuda shallow water fishes. II. Order Percomorphi, Suborder Percesoces: Atherinidae, Mugilidae, Sphyreanidae. Zoologica, **22:** 265–279.

JAANUSSON, V. 1981. Functional thresholds in evolutionary progress. Lethaia, **14:** 251–260.

JOHNSON, G. D. 1980. The limits and relationships of the Lutjanidae and associated families. Bulletin Scripps Institution of Oceanography, **24:** 1–114.

———. 1984. Percoidei: Development and relationships, pp. 464–498. *In* H. G. Moser (ed.-in-chief), Ontogeny and Systematics of Fishes. Special Publications of the American Society of Ichthyologists and Herpetologists No. 1. Lawrence, KS: Allen Press. 760 pp.

JORDAN, D. S. 1905. Guide to the Study of Fishes. Volume II. New York: Henry Holt and Co. xxii + 599 pp.

KAUFMAN, L., AND K. F. LIEM. 1982. Fishes of the suborder Labroidei (Pisces: Perciformes): Phylogeny, ecology, and evolutionary significance. Breviora. Museum of Comparative Zoology, Harvard University, **472:** 1–19.

LAUDER, G. V. 1981. Form and function: structural analysis in evolutionary morphology. Paleobiology, **7**(4): 430–442.

———. 1982a. Historical biology and the problem of design. Journal of Theoretical Biology, **97:** 57–67.

———. 1982b. Introduction, pp. xi–xlv. *In* E. S. Russell, Form and Function. A Contribution to the History of Animal Morphology. Chicago: University of Chicago Press. xlv + 383 pp.

———. 1983. Functional design and evolution of the pharyngeal jaw apparatus in euteleostean fishes. Zoological Journal of the Linnean Society of London, **77:** 1–38.

LAUDER, G. V., AND K. F. LIEM. 1983. The evolution and interrelationships of the actinopterygian fishes. Bulletin of the Museum of Comparative Zoology, Harvard University, **150:** 95–197.

LAUR, D. R., AND A. E. EBELING. 1983. Predator-prey relationships in surfperches. Environmental Biology of Fishes, **8:** 217–229.

LIEM, K. F. 1973. Evolutionary strategies and morphological innovations: cichlid pharyngeal jaws. Systematic Zoology, **22:** 425–441.

———. 1980. Adaptive significance of intra- and interspecific differences in the feeding repertoires of cichlid fishes. American Zoologist, **20:** 295–314.

———. 1986. The pharyngeal jaw apparatus of the Embiotocidae (Teleostei): A functional and evolutionary perspective. Copeia, **1986**(2): 311–323.

LIEM, K. F., AND J. W. M. OSSE. 1975. Biological versatility, evolution and food resource exploitation in African cichlid fishes. American Zoologist, **15:** 427–454.

LIEM, K. F., AND P. H. GREENWOOD. 1981. A functional approach to the phylogeny of the pharyngognath teleosts. American Zoologist, **21:** 83–101.

LIEM, K. F., AND D. B. WAKE. 1985. Morphology: Current approaches and concepts, pp. 366–377. *In* M. Hildebrand, D. Bramble, K. F. Liem, and D. B. Wake (eds.), Functional Vertebrate Morphology. Cambridge, Mass.: The Belknap Press of Harvard University Press. 430 pp.

LIEM, K. F., AND L. SANDERSON. 1986. The pharyngeal jaw apparatus of labrid fishes: a functional morphological perspective. Journal of Morphology, **187:** 143–158.

MADDISON, W. P. 1986. MacClade version 1. Program and user's manual. Privately distributed.

MADDISON, W. P., M. J. DONOGHUE, AND D. R. MADDISON. 1984. Outgroup analysis and parsimony. Systematic Zoology, **33:** 83–103.

MAYR, E. 1963. Animal Species and Evolution. Cambridge, Mass.: Belknap Press of Harvard University Press. xiv + 797 pp.

———. 1969. Principles of Systematic Zoology. New York: Columbia University Press. xxxvii + 334 pp.

———. 1976. Sibling or cryptic species, pp. 510–514. *In* E. Mayr (ed.), Evolution and the Diversity of Life. Selected Essays. Belknap Press of Harvard University Press. ix + 721 pp.

MCKAYE, K. R., T. KOCHER, P. REINTHAL, AND I. KORNFIELD. 1982. A sympatric sibling species complex of *Petrotilapia* Trewavas from Lake Malawi analysed by enzyme electrophoresis (Pisces, Cichlidae). Zoological Journal of the Linnean Society of London, **76:** 91–96.

MILLER, A. H. 1949. Some ecologic and morphologic considerations in the evolution of higher taxonomic categories, pp. 84–88. *In* E. Mayr and E. Schuz (eds.), Ornithologie als Biologische Wissenschaft. Heidelberg: Carl Winter.

MORRIS, S. L. 1982. The osteology and relationships of the Embiotocidae (Pisces). Ph.D. thesis. Oregon State University.

MORRIS, S. L., AND A. J. GAUDIN. 1982. Osteocranial development of the viviparous surfperch *Amphistichus argenteus* (Pisces: Embiotocidae). Journal of Morphology, **174:** 95–120.

MÜLLER, J. 1843. Nachtrage zu der Abhandlung uber die naturlich Familien der Fische. Archive für Naturgeschichte, **9:** 381–384.

NELSON, G. J. 1967a. Gill arches of some teleostean fishes of the families Girellidae, Pomacentridae, Embiotocidae, Labridae and Scaridae. Journal of Natural History, **1:** 289–293.

———. 1967b. Branchial muscles in some generalized teleostean fishes. Acta Zoologica, Stockholm, **48:** 277–288.

———. 1969. Gill arches and the phylogeny of fishes, with notes on the classification of vertebrates. Bulletin of the American Museum of Natural History, **141**(4): 480–552.

NELSON, G. J., AND N. I. PLATNICK. 1981. Systematics and Biogeography. Cladistics and Vicariance. New York: Columbia University Press. xi + 567 pp.

NELSON, J. S. 1984. Fishes of the World. Toronto: John Wiley and Sons. xv + 523 pp.

NORMAN, J. R. 1966. A Draft Synopsis of the Orders, Families and Genera of Recent Fishes and Fish-Like Vertebrates. 4. Trustees of the British Museum (Natural History). 649 pp.

PARENTI, L. R. 1984. A taxonomic revision of the andean killifish genus Orestias (Cyprinodontiformes, Cyprinodontidae). Bulletin of the American Museum of Natural History, **178**(2): 107–214.

PARIN, N. V. 1961. The bases for the classification of the flying-fishes (families Oxyporhamphidae and Exocoetidae). Trudy Instituta Okeanologii, Akademiya Nauk SSSR, Moskva, **43:** 92–183. Translation No. 67 Systematics Lab., NMFS, Washington.

PATTERSON, C. 1968. The caudal skeleton of Mesozoic acanthopterygian fishes. Bulletin of the British Museum of Natural History (Geology), **17**(2): 47–102.

———. 1977. Cartilage bones, dermal bones and membrane bones, or the exoskeleton versus the endoskeleton, pp. 77–121. *In* S. M. Andrews, R. S. Miles, and A. D. Walker (eds.), Problems in Vertebrate Evolution. London: Academic Press. 411 pp.

PELLEGRIN, J. 1903. Contribution a l'étude anatomique, biologique et taxonomique des poissons de la famille des cichlidés. Mémoires Société Zoologique de France, **16:** 41–402.

REGAN, C. T. 1913. The classification of percoid fishes. Annals and Magazine of Natural History, (8)**12:** 111–145.

ROGNES, K. 1973. Head skeleton and jaw mechanism in the Labrinae (Teleostei: Labridae) from Norwegian waters. Acta Universitatis Bergensis, Series Mathematica Rerumque Naturalium, **4:** 1–149.

ROSEN, D. E. 1964. The relationships and taxonomic position of the halfbeaks, killifishes, silversides, and their relatives. Bulletin of the American Museum of Natural History, **127**(5): 219–267.

———. 1973. Interrelationships of higher euteleostean fishes, pp. 397–513. *In* P. H. Greenwood, R. S. Miles, and C. Patterson (eds.), Interrelationships of Fishes. London: Academic Press. 536 pp.

———. 1985. An essay on euteleostean classification. American Museum Novitates, **2827:** 1–45.

ROSEN, D. E., AND P. H. GREENWOOD. 1976. A fourth neotropical species of synbranchid eel and the phylogeny and systematics of synbranchi-

form fishes. Bulletin of the American Museum of Natural History, **157:** 1–70.

ROSEN, D. E., AND L. R. PARENTI. 1981. Relationships of *Oryzias*, and the groups of atherinomorph fishes. American Museum Novitates **2719:** 1–25.

ROSEN, D. E., AND C. PATTERSON. 1969. The structure and relationships of the paracanthopterygian fishes. Bulletin of the American Museum of Natural History, **141**(3): 357–474.

RUSSELL, E. S. 1982. Form and Function. A Contribution to the History of Animal Morphology. Chicago: Chicago University Press. xlv + 383 pp.

SCHMITT, R. J., AND J. A. COYER. 1982. The foraging ecology of sympatric marine fish in the genus *Embiotoca* (Embiotocidae): Importance of foraging behavior in prey size selection. Oecologia, **55:** 369–378.

SIMON, H. A. 1962. The architecture of complexity. Proceedings of the American Philosophical Society, **106:** 467–482.

SIMPSON, G. G. 1944. Tempo and Mode in Evolution. New York: Columbia University Press. xvii + 237 pp.

———. 1953. The Major Features of Evolution. New York: Columbia University Press. xx + 434 pp.

———. 1959. The nature and origin of supraspecific taxa. Cold Spring Harbor Symposia on Quantitative Biology, **24:** 255–271.

SMITH, C. L., AND R. M. BAILEY. 1961. Evolution of the dorsal-fin supports of percoid fishes. Papers of the Michigan Academy of Science, Arts, and Letters, **XLVI:** 345–363.

———. 1962. The subocular shelf of fishes. Journal of Morphology, **110**(1): 1–17.

SPRINGER, V. G. 1968. Osteology and classification of the fishes of the family Bleniidae. Bulletin of the United States National Museum No. 284. 83 pp.

SPRINGER, V. G., AND W. C. FREIHOFER. 1976. Study of the monotypic fish family Pholidichthyidae (Perciformes). Smithsonian Contributions to Zoology, **216:** 1–43.

STANLEY, S. M. 1968. Post-paleozoic adaptive radiation of infaunal bivalve molluscs—a consequence of mantle fusion and siphon formation. Journal of Paleontology, **42**(1): 214–229.

———. 1975. A theory of evolution above the species level. Proceedings of the National Academy of Sciences, **72**(2): 646–650.

———. 1979. Macroevolution. Pattern and Process. San Francisco: W. H. Freeman and Co. xi + 332 pp.

STEVENS, P. F. 1980. Evolutionary polarity of character states. Annual Review of Ecology and Systematics, **11:** 333–358.

STIASSNY, M. L. J. 1980. The anatomy and relationships of two genera of African cichlid fishes. Ph.D. thesis, University of London.

———. 1981. The phyletic status of the family Cichlidae (Pisces, Perciformes): A comparative anatomical investigation. Netherlands Journal of Zoology, **31:** 275–314.

———. 1982. The relationships of the neotropical genus *Cichla* (Perciformes, Cichlidae): a phyletic analysis including some functional considerations. Journal of the Zoological Society of London, **197:** 427–453.

———. 1986. The limits and relationships of the acanthomorph teleosts. Journal of Zoology, London (B), **1:** 411–460.

———. in press. Cichlid intrafamilial relationships and the placement of the Neotropical genus *Cichla* (Perciformes: Labroidei). Journal of Natural History.

STRAUSS, R. 1984. Allometry and functional feeding morphology in haplochromine cichlids, pp. 217–229. *In* A. A. Echelle and I. Kornfield (eds.), Evolution of Fish Species Flocks. Orono: University of Maine at Orono Press. 257 pp.

SZALAY, F. S. 1981. Functional analysis and the practice of the phylogenetic methods as reflected by some mammalian studies. American Zoologist, **21:** 37–45.

SWOFFORD, D. L. 1985. Phylogenetic Analysis Using Parsimony. Version 2.4 User's Manual. Champaign: Illinois Natural History Survey.

TARP, F. H. 1952. A revision of the family Embiotocidae (the surfperches). California Department of Fish and Game Fish Bulletin, No. **88:** 1–99.

TRAVERS, R. A. 1981. The interarcual cartilage: a review of its development, distribution and value as an indicator of phyletic relationships in euteleostean fishes. Journal of Natural History, **15:** 853–871.

———. 1984a. A review of the Mastacembeloidei, a suborder of synbranchiform teleost fishes. Part I: Anatomical descriptions. Bulletin of the British Museum of Natural History, **46:** 1–133.

———. 1984b. A review of the Mastacembeloidei, a suborder of synbranchiform teleost fishes. Part II: Phylogenetic analysis. Bulletin of the British Museum of Natural History, **47**(2): 83–150.

TREWAVAS, E. 1973. On the cichlid fishes of the genus *Pelmatochromis* with proposal of a new genus for *P. congicus*; on the relationship between *Pelmatochromis* and *Tilapia* and the recognition of *Sarotherodon* as a distinct genus. Bulletin of the British Museum of Natural History (Zoology), **25**(1): 3–26.

VANDEWALLE, P. 1973. Osteologie caudale des Cichlidae (Pisces: Teleostei). Bulletin Biologique de la France et de la Belgique, **107:** 275–289.

VERMEIJ, G. 1973. Adaptation, versatility, and evolution. Systematic Zoology, **22:** 466–477.

VRBA, E. S. 1980. Evolution, species and fossils: How does life evolve? South African Journal of Science, **76:** 61–84.

WATROUS, L. E., AND Q. D. WHEELER. 1981. The outgroup comparison method of character analysis. Systematic Zoology, **30:** 1–11.

WHITE, M. J. D. 1978. Modes of Speciation. San Francisco: W. H. Freeman and Co. vii + 455 pp.

WILEY, E. O. 1981. Phylogenetics. The Theory and Practice of Phylogenetic Systematics. New York: John Wiley and Sons. xv + 439 pp.

WINTERBOTTOM, R. 1974. A descriptive synonomy of the striated muscles of the Teleostei. Proceedings of the Academy of Natural Sciences of Philadelphia, **125**: 225–317.

WITTE, F. 1984. Ecological differentiation in Lake Victoria haplochromines: comparison of cichlid species flocks in African lakes, pp. 155–167. *In* A. A. Echelle and I. Kornfield (eds.), Evolution of Fish Species Flocks. Orono: University of Maine at Orono Press. 257 pp.

YAMAOKA, K. 1978. Pharyngeal jaw structure in labrid fish. Publications of the Seto Marine Biological Laboratory, **24**(4/6): 409–426.

———. 1980. Some pharyngeal jaw muscles of *Calotomus japonicus* (Scaridae, Pisces). Publications of the Seto Marine Biological Laboratory, **25**(5/6): 315–322.

APPENDIX 1

Data Matrix Used in Character Analysis

Taxa/Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Plesiomorphic	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cichlidae	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1
Embiotocidae	1	1	1	0	0	0	0	1	1	1	0	0	0	1	1
Labridae	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1
Pomacentridae	1	1	1	1	1	1	1	0	0	0	0	0	0	1	0

The characters are:

1. LPJ with no trace of a central suture, and with pharyngeal teeth implanted directly over the midline.
2. Urohyal articulates with basibranchial one.
3. Absence of musculus cranio-pharyngobranchialis 2 muscle.
4. LPJ "Y-shaped" with short body and elongate lateral horns.
5. Obliquus ventralis IV and rectus ventralis V insert separately onto the semicircular ligament system.
6. Basibranchial one bears a large keel-like ventral extension.
7. Uroneural fused with the urostyle.
8. Second pharyngobranchial toothplate absent.
9. Fourth upper toothplate either markedly reduced or entirely lacking.
10. Interarcual cartilage absent.
11. Reduced number of caudal epurals.
12. Two or fewer predorsal bones.
13. Endopterygoid shelf absent and adductor arcus palatini inserts onto medial face of the suspensorium.
14. Extrascapular bone fused to the parietal.
15. Hemal arch of the antepenultimate caudal vertebrae fused with the centrum.

APPENDIX 2

Abbreviations Used in Figures

AD5	Adductor 5
ART.Z	Articulation zone
BB1–4	Basibranchial 1–4
BHY	Basihyal
CB1–5	Ceratobranchial 1–5
CL	Cleithrum
CT	Connective tissue
"EHR"	"Epihemal ribs"
EP1–4	Epibranchial 1–4
EPR	Epipleurals
INTARC.C	Interarcual cartilage
HBR	Hypobranchial
L.BB3/UHY	Basibranchial3/urohyal ligament
LE4	Fourth levator externus muscle
LE_4 + OP	Fourth levator externus and obliquus posterior
LP	Levator posterior muscle
LPJ	Lower pharyngeal jaw
LT. HORN	Lateral horn
OBL IV	Obliquus ventralis IV
OP	Obliquus posterior muscle
MC. P2	Cranio-pharyngobranchialis 2
MT. E2	Transverse epibranchialis 2
MT. P2	Transversus pharyngobranchialis 2
NC. AP	Neurocranial apophysis
PB1-3	Pharyngobranchial 1–3
PB3-TP	Pharyngobranchial 3 toothplate
PB2-3-TP	Toothplate of PB 2–3
PB3-FC	Articulation facet of PB3
PHC.E	Pharyngocleithralis externus
PHC.I	Pharyngocleithralis internus
PHY	Pharyngohyoideus
PR	Pleural rib
REC.V	Rectus ventralis V
SEMICIRC.LIG	Semicircular ligament system
tA_1	Tendon of A_1 division of adductor mandibulae
TDP	Transversus dorsalis posterior
TV IV-V	Transversus ventralis IV–V
UHY	Urohyal
UP4	Fourth upper toothplate

(US ISSN 0027-4100)

Bulletin OF THE
Museum of
Comparative
Zoology

Systematics and Levels of Covariation in *Cerion* from the Turks and Caicos Islands

STEPHEN JAY GOULD and DAVID S. WOODRUFF

HARVARD UNIVERSITY
CAMBRIDGE, MASSACHUSETTS, U.S.A.

VOLUME 151, NUMBER 6
14 SEPTEMBER 1987

(US ISSN 0027-4100)

PUBLICATIONS ISSUED OR DISTRIBUTED BY THE MUSEUM OF COMPARATIVE ZOOLOGY HARVARD UNIVERSITY

Breviora 1952–
Bulletin 1863–
Memoirs 1864–1938
Johnsonia, Department of Mollusks, 1941–
Occasional Papers on Mollusks, 1945–

SPECIAL PUBLICATIONS.

1. Whittington, H. B., and E. D. I. Rolfe (eds.), 1963. Phylogeny and Evolution of Crustacea. 192 pp.
2. Turner, R. D., 1966. A Survey and Illustrated Catalogue of the Teredinidae (Mollusca: Bivalvia). 265 pp.
3. Sprinkle, J., 1973. Morphology and Evolution of Blastozoan Echinoderms. 284 pp.
4. Eaton, R. J. E., 1974. A Flora of Concord. 236 pp.
5. Rhodin, G. J., and K. Miyata (eds.), 1983. Advances in Herpetology and Evolutionary Biology: Essays in Honor of Ernest E. Williams. 745 pp.

Other Publications.

Bigelow, H. B., and W. C. Schroeder, 1953. Fishes of the Gulf of Maine. Reprint.

Brues, C. T., A. L. Melander, and F. M. Carpenter, 1954. Classification of Insects.

Creighton, W. S., 1950. The Ants of North America. Reprint.

Lyman, C. P., and A. R. Dawe (eds.), 1960. Symposium on Natural Mammalian Hibernation.

Ornithological Gazetteers of the Neotropics (1975–).

Peters' Check-list of Birds of the World, vols. 1–16.

Proceedings of the New England Zoological Club 1899–1948. (Complete sets only.)

Publications of the Boston Society of Natural History.

Price list and catalog of MCZ publications may be obtained from Publications Office, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, 02138, U.S.A.

This publication has been printed on acid-free permanent paper stock.

SYSTEMATICS AND LEVELS OF COVARIATION IN *CERION* FROM THE TURKS AND CAICOS ISLANDS

STEPHEN JAY GOULD[1] AND DAVID S. WOODRUFF[2]

ABSTRACT. *Cerion*, the most morphologically diverse of all pulmonate genera, has been vastly oversplit in such a way that existing names form an incoherent pattern of variation within and among islands. We have reduced the 300-odd taxa of northern Bahamian *Cerion* to a half-dozen species with consistent and predictable distributions. This study represents our first attempt to apply our ecogeographic and biometric methods to the different *Cerion* fauna of the southeastern Bahamas.

The dozen available names, inconsistently distributed about the islands of the Turks and Caicos banks, reduce to three valid species: *Cerion regina*, present on all islands as Turks and Caicos representative of the "tapering morphotype," the predominant and characteristic *Cerion* of this entire region; *C. lewisi*, a Cuban migrant restricted to islands of the western Caicos Bank; and *C. blandi*, misattributed to the *C. glans* complex in the past, but actually an immigrant population of the *C.* (*Umbonis*) stock, confined to Salt Cay on the Turks Bank and hybridizing with local *C. regina*.

Biometric patterns based on factor analyses of mean vectors for all samples reveal order without exception at a series of descending levels. Clustering of samples can be interpreted as results of meaningful patterns in covariance among measures defining the axes. At the most inclusive level of all samples on all islands, each of three principal axes captures the distinctive morphological features of a taxon. Therefore, axes reflect taxonomic diversity and the contingent histories of migrations. At the next lower level of variation (among samples within *C. regina* on all islands), island groups are distinguished by patterns of covariation that express developmental rules of growth and allometry within a coherent *Cerion* ground plan, not the accidents of history revealed in the higher-level analysis among taxa. A smooth morphometric cline, connecting all islands of the Caicos Bank, unites the two major taxa of previous interpretation into a continuous array, and forms the basis for our decision to synonymize all samples of the tapering morphotype as *C. regina*. At a third level of variation (*C. regina* within our best-sampled island of South Caicos), we detect coherence based upon geometric constraints of growth for any coiled shell. Finally, specimens within samples follow similar patterns of covariance, indicating that general rules of growth apply to the conceptually different styles of within- and among-sample variation.

I. The Problem and Promise of *Cerion*

Copious variation in genetically-resolvable patterns of shell coloration has secured for several pulmonate genera the status of evolutionary "classics" (Cain and Currey, 1963 on *Cepaea*; Crampton, 1916, 1925, 1932 and Murray and Clarke, 1980 on *Partula*; Gulick, 1905 and later studies on Hawaiian *Achatinella*, for example). Yet, although remarkable variation in morphology also distinguishes several pulmonate genera from most other mollusks, this source of insight has not been well exploited by evolutionary biologists—in part because the classic genera for studies of color are not particularly variable in form.

Cerion, a widespread West Indian land snail favoring coastal, carbonate substrates, may be the most morphologically diverse of all pulmonate genera, with variation in shell height from 5 to 70 mm, and in shape from pencils to golf balls. We understand the formal basis for this geometric diversity (Gould, 1984b; Gould and Woodruff, 1986; Woodruff and Gould, 1980), but little of its genetic and developmental foundation. The potential for such unparalleled diversity arises from two aspects of growth: first, the complex, ba-

[1] Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138.

[2] Department of Biology C-016, University of California, San Diego, La Jolla, California 92093.

sically tripartite allometry of all *Cerion* ontogenies (a juvenile button or triangle, followed by an adult "barrel" with little increase in width accompanying major growth in height, and a final change in coiling before secretion of the definitive adult lip); second, the ordering of growth patterns into several interacting but mutually dissociable covariance sets of coordinated characters. This complex allometry provides great scope for translating small heterochronic effects into major changes in adult form, while the potential independence of covariance sets enjoins both forced correlations within sets (further translating small inputs into complex outputs) and substantial play for novel combinations (by independent change between sets). *Cerion*, in short, is a premier subject for students of form.

Yet *Cerion*'s promise has been impeded by two related "myths" propagated by its traditional literature (particularly Maynard, 1889; Maynard and Clapp, 1919–26). First, *Cerion*'s extreme lability in form has inspired the construction of a bloated taxonomy of some 600 taxa, about half from the Bahamas where we have concentrated our studies (see Clench, 1957). Nearly all named taxa of *Cerion* hybridize freely, and few genuine biological species exist. The second *Cerion* myth holds that the geographic distribution of these formally designated taxa forms a basically incoherent spread, implicating capricious and distant transport by hurricanes as the primary mode of colonization. Admittedly, the placement of existing names on maps implies chaos of this sort, but the traditional taxonomy is fundamentally erroneous (Gould and Woodruff, 1978, 1986, for example).

We have been studying the systematics and biogeography of Bahamian *Cerion* for more than a decade (see literature cited) and have been able to refute these two myths by systematic revision and synonymization of invalid taxa. In our simplified system of biological taxa mapped and studied in the field, the chaos of traditional names breaks down to be replaced by clear order and stable pattern, temporally and spatially, in the distribution of Bahamian *Cerion* among islands.

We have detected order at two basic levels of variation, and have portrayed this coherence primarily by the study of covariance sets, or groups of characters correlated by the general geometries of snail growth and the particular allometries of *Cerion*. We find, first, sensible order within taxa, based upon clines defined geographically (Gould and Paull, 1977 for *C. striatellum*) or ecologically (Gould and Woodruff, 1986 on dwarfing in *C. gubernatorium*), or upon small-scale but discontinuous differentiation among islands (Gould and Woodruff, 1978 on *C. bendalli* in Abaco and Grand Bahama; Gould, 1984a on *C. uva* in Aruba, Bonaire and Curaçao). Second, we have demonstrated consistency in the distribution and interaction of taxa within regions. We find the same forms (or "morphotypes," for we do not know their genealogies) in the same settings from island to island within regions ("ribby" *Cerion* on bank-edge coasts, and "mottled" *Cerion* on bank-interior coasts and island interiors on all major islands of the northern Bahamas, Gould and Woodruff, 1978, 1986). When anomalous taxa invade regions, they occupy restricted areas superimposed upon the underlying predictability of indigenous forms (for example, incursions of the subgenus *C.* (*Umbonis*) into bounded portions of the "ribby" coastal range on eastern Andros, Cat and Long Islands).

II. A Strategy of Research

We have reached the half-way point in our systematic and evolutionary revision of Bahamian *Cerion*. We have studied all major islands of the northern Bahamas (Little and Great Bahama Bank) and have found on each of the eight primary territories (Grand Bahama, Abaco, Andros, New Providence, Eleuthera, Cat, Exuma, and Long Island) the same basic distribution of bank-edge (usually east coast)

"ribby" and bank-interior (usually west coast) "mottled" *Cerion* described above (see Gould and Woodruff, 1986 for summary). In addition, at least two islands (Cat and Eleuthera) harbor relict populations of the major Sangamon taxon from the ca. 120,000 year b.p. dunes of these islands—smooth, white, thick-lipped *C. agassizi*. Finally, a few local incursions of other taxa, usually of the subgenus *C.* (*Umbonis*), have been recorded. The identification of this consistent pattern has permitted us to reduce the bloated taxonomy of Bahamian *Cerion* by more than half, synonymizing some 300 invalid names to a half-dozen or so biological species.

We now extend this program to the genuinely different *Cerion* faunas of the southeastern Bahamas (Inagua, Mayaguana, Crooked-Acklins, and the geographically linked though politically independent Turks and Caicos). The major difference between the two regions is evident by inspection of museum collections. Whereas the ribby-mottled distinction unlocks the northern Bahamas, the main *Cerion* morphotype of the southern Bahamas is an ovate-triangular, generally smooth and white form known by a plethora of names—*C. columna* and *C. christophei* on Inagua, *C. regium* on Castle Island, *C. piratarum* on Mayaguana, *C. regina* on Grand Turk, *C. caicosense* on South Caicos, for example—but sufficiently similar from place to place to provoke a strong suspicion that their underlying unity might provide a key to the southern region. This study is a first attempt to apply the methods that we used successfully in the northern Bahamas to the different fauna of the southern islands, in particular to variation within the "tapering" morphotype (as we shall call it).

We choose the Turks and Caicos islands for this first attempt for two reasons. First, these banks are, geographically speaking, the eastern outliers of the Bahamian complex. Their *Cerion* faunas are simpler than those of larger, more central islands like Inagua. We have had success in our previous work by beginning with sparser faunas of peripheral areas (Gould and Paull, 1977; Gould, 1969a, 1984a) and working towards greater, central complexity (Gould and Woodruff, 1986). Second, several names have been applied on various islands of the Turks and Caicos to populations that may all belong to the tapering morphotype. If we can resolve the current set of unrelated names into a pattern of coherent variation, then we may hope that the southern Bahamas will also yield to a replacement of taxonomic chaos by biological order. In this case, a revision of the entire Bahamian *Cerion* fauna will be within our grasp.

III. The Current Status of the Turks and Caicos *Cerion* Fauna

The available nomenclature for Turks and Caicos *Cerion* provides an excellent example of the systematic problem (systematic, that is, in both technical and vernacular senses) besetting this genus. The Turks and Caicos, spared visits by the most ardent splitters among *Cerion* aficionados, are relatively "underrepresented" by *Cerion* species. Clench's (1957) catalogue lists nine taxa, and two have been added since (Clench, 1961). The existing descriptions give no hint of any order or pattern in the distribution of these supposed taxa on the various islands.

The first eight names were bestowed by Pilsbry and Vanatta in their short paper of 1895 and their catalogue of 1896. Pilsbry, impressed by Maynard's demonstration that the internal teeth and lamellae of *Cerion* shells had taxonomic value, engaged Vanatta to section shells in the extensive collection of the Academy of Natural Sciences of Philadelphia. He thought, in so doing, that he had "brought to light" many new species. In particular, he distinguished for the first time a "Turk's Island" (1895, p. 208) species of *Cerion* from other taxa of the tapering morphotype. He named this first Turks and Caicos species *C. regina* (1895, p. 208), distinguishing it from *C. columna* of Inagua by its more

triangular profile (*C. columna*, as its name implies, is more parallel-sided); from *C. regium* of Castle Island by its smaller size and less thickened apertural lip (as compared with the thick lip of *C. regium*, described in a disparaging and mildly racist manner by Pilsbry and Vanatta as "a lip of quite Ethiopian characteristics"); and from *C. lentiginosum* and *C. album* of Rum Cay by its smoother shell (for the Rum Cay species are costate on their early whorls). Pilsbry and Vanatta then named five subspecies of *C. regina*, in order (pp. 208–209) as *C. r. percostatum* for ribbed shells; *C. r. comes* (literally, the pretty queen) for shells "heavily streaked and blotched with chestnut brown"; *C. r. Swiftii* for smaller, thinner and more triangular shells; *C. r. eucosmium* for smooth, glossy shells with livid, pinkish-brown streaks; and *C. r. brevispira* for short, compact shells. All these names were applied to shells from "Turk's Island," presumably Grand Turk of modern nomenclature. All names refer to common variants of color, ribbing, and size (with engendered covariances in shape) now recognized as the major and pervasive paths of variation throughout the genus.

Pilsbry and Vanatta then recognized a second species from "Turk's Island" as *Cerion incanoides* (1895, p. 209). They noted that "this species belongs clearly to the group of *C. regina*, *lentiginosum*, etc." (loc. cit.), but established a separate taxon to recognize the thin and smooth shell of this form. We do not understand why they made this distinction because, at least to us, collections of *C. incanoides* differ no more from *C. regina* than do several of the *C. regina* subspecies among themselves.

In their 1896 catalogue, a landmark attempt to systematize the entire genus, Pilsbry and Vanatta listed the Turks and Caicos taxa included under and allied with *Cerion regina*. They then named, as *C. blandi* (1896, listed on p. 324, described on p. 334), a genuinely different *Cerion* from this region. They included this thick and solid, small to medium sized, cylindrical rather than triangularly shaped, and strongly ribbed shell in the group of *Cerion glans*, the typical ribby *Cerion* of the northern Bahamas. In so doing, they made an interesting error. *C. blandi*, confined to small Salt Cay of the Turks group, represents an incursion of the distinctive subgenus *C.* (*Umbonis*) that has hybridized to varying degrees with *C. regina* stocks. *C.* (*Umbonis*) has distinctively wavy ribs and incised spiral lines, but these characters are often muted in hybrid forms. In particular, as in *C. felis* of Cat Island and *C. glans irregulare* of northern Andros (both hybrids between an umbonid and *C. glans*), most specimens lack the incised lines and bear strong ribs only moderately wavy. In this "diluted" state, shells of *C. blandi* do superficially resemble standard ribby *Cerion*. Indeed, Pilsbry and Vanatta glimpsed the true status of *C. blandi* in adding to the end of the description: "but the ribs are conspicuously different, peculiarly rough and unfinished, somewhat like *C. felis*" (1896, p. 334). *C. felis* is a *C.* (*Umbonis*) hybrid from Cat Island.

In 1937, Clench described the first *Cerion* from the Caicos islands, establishing the new species, *C. caicosense*. Clench recognized its allegiance with *C. incanoides* and the *C. regina* group, but felt that smaller size, whiter color, and proportions of the apertural teeth (parietal smaller and columellar longer) warranted a new species. We shall show that the Caicos populations, particularly from South Caicos, are distinct biometrically, but for none of the reasons identified by Clench, since all his differentia show overlap with mean values from Turks island populations.

In 1961, Clench wrote a summary paper on land shells of the Turks and Caicos. He properly lumped all previous names for the *C. regina* group, except his own *C. caicosense*, into *C. regina* itself (1961, p. 250), not primarily for morphological reasons, but because all had been described from Grand Turk, and the necessary criterion of geographic distinction for subspecies had not therefore been met. He

retained *C. caicosense* primarily for its geographic separation.

Clench then added two new taxa. First, he described as *C. utowana abbotti* (1961, p. 251) shells from several islands on both Turks and Caicos banks that differed from *C. regina* primarily in the parallel-sided, rather than tapering form of the adult shell. This decision baffles us for two reasons. First, we do not know why he designated these shells as a subspecies of the East Plana Cay form *C. utowana* since its relationships, to us at least, seem so clearly with the local *C. regina* forms. Our biometric work, based on characters that Clench used to distinguish this taxon, places these populations squarely within the *C. regina* field (see section VI C). Second, we do not understand why he distinguished this taxon at all since several populations within *C. regina* share this morphospace in the common continuum from quite triangular to quite cylindrical shells.

Clench then designated as *C. lewisi* (1961, p. 255) an uncontestably different *Cerion* from several islands in the northwestern Caicos. This very thin, strongly mottled, cylindrical, smooth shell looks nothing like any other Turks and Caicos *Cerion*, yet cannot be distinguished conchologically from the highly distinctive *C. lepidum* from nearby parts of Cuba. We do not doubt, as Clench also concluded, that *C. lewisi* is a Cuban emigrant restricted to a few islands of the Caicos Bank.

The existing taxonomy therefore leaves us confused. *C. blandi* (an umbonid incursion probably phasing itself out by hybridization), and *C. lewisi* (a Cuban emigré) are distinct and locally restricted products of probably recent immigration. The prevalent local form, the tapering morphotype that gives the southern Bahamas its *Cerion* "signature," now carries four species names of uncertain status. Pilsbry and Vanatta's *C. regina* has priority, but *C. incanoides* (though synonymized with *C. regina* by Clench) also refers to Turk Island forms. *C. caicosense* has been applied to Caicos island populations, but the basis of its distinction remains unclear. Finally, *C. utowana abbotti* has been described from both banks, but with no evident differences from the *C. regina* incumbents. Moreover, no one has ever claimed any consistent or simplifying pattern in the geographic distribution of the *C. regina* complex in the Turks and Caicos islands. A resolution of *Cerion* on these banks must evidently center on a proper characterization and mapping of morphological differences within the *C. regina* group.

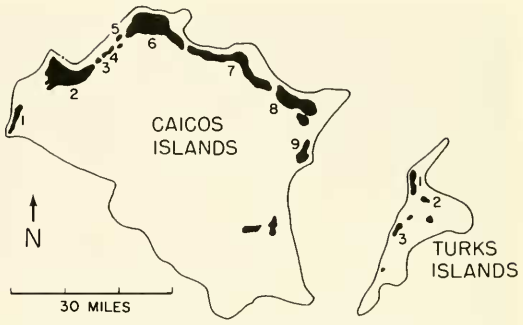


Figure 1. Islands of the Turks and Caicos banks. Turks: 1, Grand Turk. 2, Long Cay. 3, Salt Cay. Caicos: 1, West Caicos. 2, Providenciales. 3, Pine Cay. 4, Water Cay. 5, Parrot Cay. 6, North Caicos. 7, Grand Caicos. 8, East Caicos. 9, South Caicos.

IV. Materials and Methods

We have based our systematic revisions of *Cerion* on biometric and genetic studies of animals collected personally in the field as we map the ecologic and biogeographic distribution of *Cerion*. (We have often, as here, augmented our own material with samples from Museum collections representing populations no longer extant or difficult of access.) In May–June, 1978, we visited the Turks and Caicos to study the geographic and ecological distribution of variation in the tapering morphotype. We collected extensively on South Caicos, sampling every population that we could locate; we then sampled less fully on the largest and most distant island of the Caicos Bank (Providenciales), and on the major island of the Turks Bank (Grand Turk).

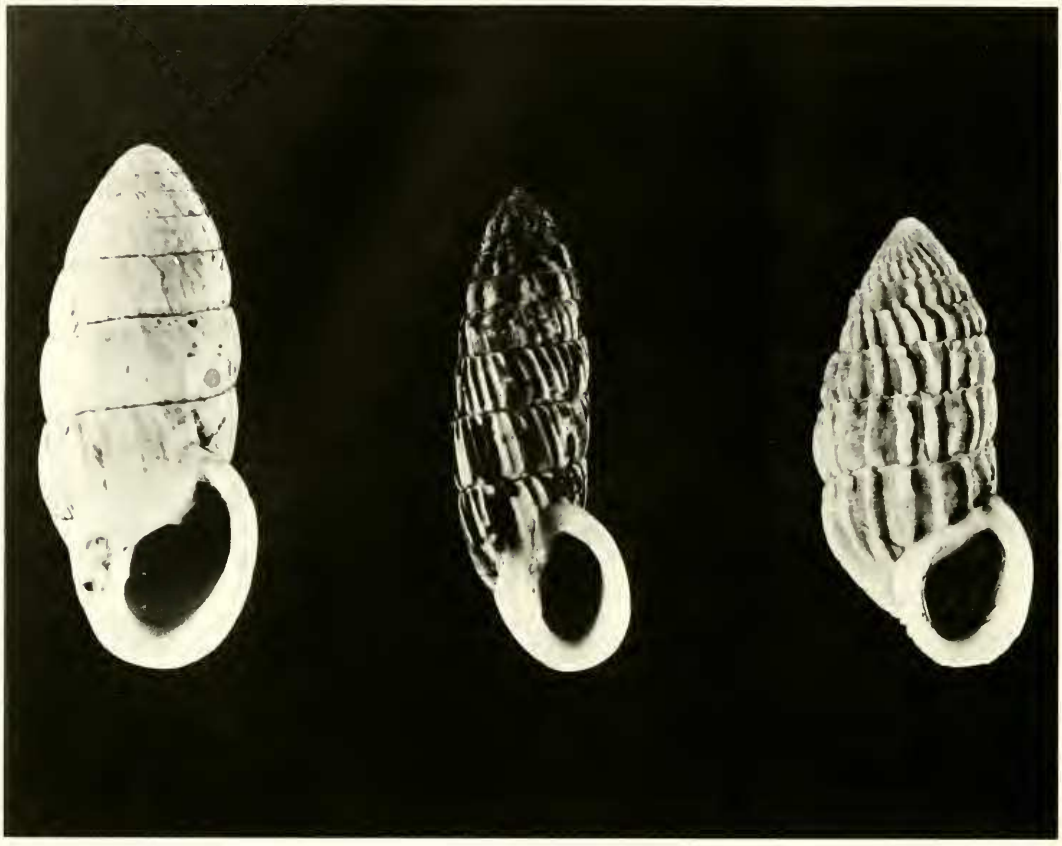


Figure 2. Representative specimens of the three *Cerion* taxa of the Turks and Caicos. Left, *C. regina* from South Caicos, our sample 753. Middle, *C. lewisi* from Parrot Cay, Caicos Bank, MCZ No. 221566. Right, *C. blandi* from Salt Cay, Turks Bank, MCZ No. 220913. Note characteristic *C.* (*Umbonis*) features of *C. blandi*: wavy ribs and incised lines perpendicular to the ribs. The *C. regina* specimen is 34.0 mm high.

We used 29 of our own samples for our morphometric analysis, 23 living and six subfossil. These include 19 from South Caicos (14 living, five subfossil), seven from Grand Turk (six living and one subfossil), and three from Providenciales (all living).

We then selected 32 additional samples for biometric analysis from the collections of the Department of Mollusks at the Museum of Comparative Zoology. These include 15 samples of the tapering morphotype (13 from islands that we had not visited, and two from South Caicos—the paratypes of *C. caicosense*, and *C. utowana abbotti*, both taxa that we regarded as ripe for synonymy). In addition, we measured ten samples of *C. blandi* and its hybrids with tapering forms, all from Salt Cay on the Turks Bank, and seven samples of *C. lewisi* from the western Caicos (West Caicos, Providenciales, Pine Cay, Water Cay, Parrot Cay and Ft. George's Cay). Thus, our set of 62 samples represents all taxa (including types and paratypes, where available), on all islands of their recorded and available distribution. Samples are listed individually in the appendix with their field or museum numbers and their location. Figure 1 shows the islands of both banks, while Figures 2 and 3 display the range of form within the Turks and Caicos *Cerion* fauna (Fig. 2 the contrast among

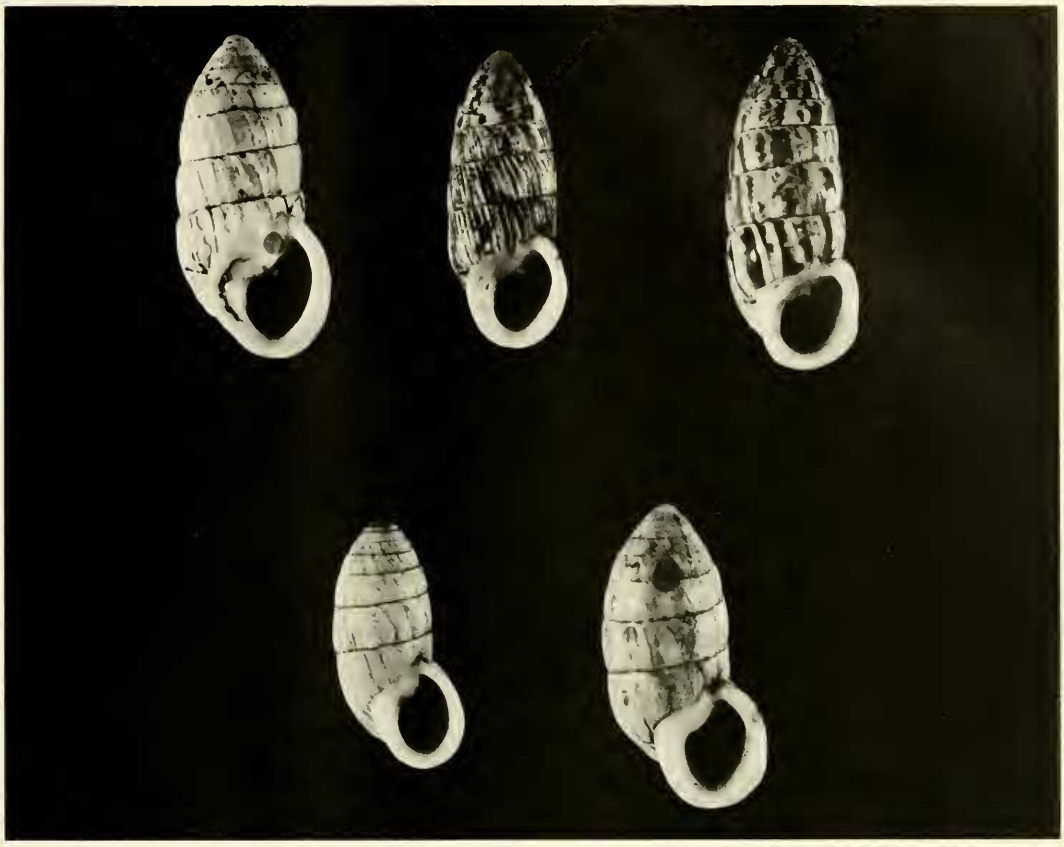


Figure 3. Representative specimens for variation within *C. regina.* Top row, the three islands represented in our personal collections. Left, South Caicos from sample 753. Note the relatively squatter apex—the key defining feature of South Caicos populations. Middle, more apically pointed, finely ribbed and mottled specimen from Providenciales, sample 771. Right, large and apically pointed specimen from Grand Turk, sample 781. Bottom row, representative specimens from paratype samples of two other designated species from South Caicos, both in our view synonyms of *C. regina.* Left, *C. caicosense.* Right, *C. utowana abbotti.* The upper row left specimen is 33.5 mm high.

the three recognized taxa; Fig. 3 the range of variation within the tapering morphotype, here treated as a single species *C. regina*).

For the biometric analysis, we selected 20 adult specimens at random from each sample and measured, for each shell, 18 characters and four additional derived ratios; this study therefore rests upon more than 20,000 direct measurements upon some 1,200 specimens in 61 samples. We have followed the protocol for measurement and analysis used in our recent work (especially Gould and Woodruff, 1986, explained more fully in Gould and Woodruff, 1978), and will not repeat the details here. Table 1 describes and lists the characters, and Figure 4 displays the points for measurements of the aperture and last whorl. The 22 measures used here include 19 of our previous set of 21 (excluding number of ribs on the 4th and 6th whorls because smooth shells of the tapering morphotype lose their juvenile ribs by this stage), plus three basic indices of shell shape (height to width ratios of the protoconch, of the final adult shell, and at the end of the fourth postprotoconch whorl) found

TABLE 1. BRIEF DESCRIPTION OF MEASURES USED IN THIS STUDY (GIVEN IN ORDER OF ARRAY IN SUBSEQUENT TABLES).

1. PROWID	Width of the protoconch
2. FOURWID	Width of shell at the end of the fourth whorl
3. NUMWHO	Total number of whorls, counting from the end of the protoconch as zero
4. RIBDENS	Number of ribs in 50 micrometer units at the end of post protoconch whorl 1
5. LENGTH	Total length of the shell
6. WIDTH	Total width of the shell
7. PROHT	Height of the protoconch
8. FOURHT	Height of shell at the end of the fourth whorl
9. FRSXHT	Height of shell from the end of the fourth to the end of the sixth whorl
10. UMBWID	Maximum width of the umbilicus
11. LIPWID	Maximum width of the lip
12. LIPTHK	Maximum thickness of the lip
13. APHT	Height of the aperture AB′ of Fig. 4
14. APWID	Width of the aperture C′D of Fig. 4
15. APROT	Projecture of apertural lip beyond outline of previous whorls, C″D of Fig. 4
16. EC	Distance from last suture to umbilical border of aperture, measured perpendicular to the suture, EC of Fig. 4
17. FA	Distance from last suture to parietal border of aperture, measured perpendicular to the suture, FA of Fig. 4
18. APTILT	The ratio EC/FA, a measure of the tilt of the aperture
19. WEIGHT	Weight of the shell
20. HWRATIO	The ratio of height to width of the shell, measures 4/5
21. PRORAT	Width/height ratio of the protoconch, measures 1/7
22. FOURRAT	Width/height ratio of the shell at the end of the fourth whorl, measures 2/8

useful in our study of sinistral *Cerion* (Gould, Young and Kasson, 1985). The mean values for all measures in all samples are given in the appendix.

Our measures are chosen to record the major shell characters used to make taxonomic distinctions, including sizes and shapes of protoconch, adult shell, and intermediate whorls; size, form and orientation of the aperture and umbilicus; ribbing and shell thickness; and size and form of the apertural lip. We have also included measures that will permit a reconstruction of basic coiling geometries, following both the analytical schemes of Raup (1966, for example) and the actual, more complex allometries of *Cerion*. *Cerion* is a nearly ideal animal for biometric research. The transition from protoconch to later growth is clearly marked, providing a clear and natural criterion for numbering whorls. Unlike most mollusks, *Cerion* possesses a definitive adult form; as growth reaches its termination, the direction of coiling shifts, the shell overgrows its previous whorls slightly, and then deposits an expanded and thickened adult lip, ceasing all growth thereafter. Thus, we can measure the adult size of *Cerion* shells, without confounding ontogenetic and static variation—a primary source of confusion in most biometric studies of snails.

Two aspects of our research program suggest a factor analytic approach as most appropriate for our analysis: first, because we wish to explore the distribution of samples in the general *Cerion* morphospace (rather than trying to test distinctions, taxonomic or otherwise, previously proposed); second, because our primary interest in the inductive study of morphology centers upon covariance sets, or groups of associated characters often flagged so well by various rotations of factor axes.

Consequently, we have portrayed each sample by its vector of means (see appendix), submitted these vectors to transformations that weight characters equally (percent-range), normalized the vectors to equal length (so that allometric effects will be expressed as shape and simple size difference will not swamp more subtle associations), and then performed our factor analyses on the transformed matrix of mean vectors. (Our analyses are in the less usual, or "inverted," Q-mode format, with loadings as samples and scores as variables, rather than in the more conventional

R-mode—see justification and empirical demonstration of equivalency between the modes in Gould and Woodruff, 1978, 1986.)

The problems presented by variation among *Cerion* samples of the Turks and Caicos may be conceptualized as a descending series of levels, each posing different questions and capturing different information. First, the positioning of all samples in a general morphospace to demonstrate the role of historical contingency in shaping the fauna by bringing two allochthones (the umbonid *C. blandi* and the Cuban import *C. lewisi*) into primary territory of the tapering morphotype. Second, the positioning of tapering samples within the morphospace set by the tapering morphotype itself to see whether any simplification of pattern might replace the current, chaotic taxonomy. Third, the positioning of samples from South Caicos alone within their own morphospace to explore, for our best and most abundantly sampled island, any order in local variation that would probably be swamped by inter-island and inter-taxon effects at the higher two levels. Fourth, and finally, the ordering of specimens within samples (this last being, of course, a break with, rather than a smooth descent from, the previous three levels, since it treats within-sample variation of specimens rather than between-sample variation of mean vectors).

We are interested not only in relationships among objects (as discussed above) but also in the associations of variables that build major dimensions of the morphospace, for the covariance sets thus defined act as constraining channels of variation that both limit the kinds of variation expressed, and also provide opportunity for generating large and diverse changes of form from small inputs (via correlated consequences). The tension between these superficially contradictory but linked themes of limitation and amplification defines *Cerion*'s major interest to students of morphology.

We complemented the biometric study with a survey of genetic variation in snails

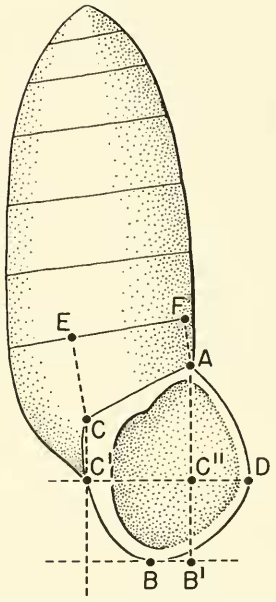


Figure 4. Sketch showing points that define our measures of the aperture. See Table 1.

of the tapering morphotype. Our survey involved more than 520 individual adult snails representing 16 populations distributed among the islands as follows: Providenciales: 2, South Caicos: 13, Grand Turk: 1. One population from South Caicos (site 758) was represented by two subsamples: 758T from a single coconut palm tree and 758 from the surrounding grass and shrubs. In most cases the same individual animals were used for both conchological and genetic study. All samples were taken by searching an area of typically 10 m^2 (a fraction of the neighborhood size) and collecting every adult encountered.

Genetic characterization was based on an examination of individual variation in 16 proteins (Table 2) extracted from foot-muscle tissue. Variation was detected by horizontal starch gel electrophoresis under conditions we have described elsewhere (Gould and Woodruff, 1986; Woodruff, 1975). Using the BIOSYS-1 computer program (Swofford and Selander, 1981) we calculated allele frequencies for each sample together with measures of genetic variation including mean number of alleles per

Table 2. Enzyme systems analyzed in Turks and Caicos *Cerion*.

Protein name (E.C. Number)	Abbreviation	Loci	Conditions*
Aspartate aminotransferase (2.6.1.1)	*Aat*	1	A
Ceruloplasmin	*Crp*	1	A
Esterase α-naphthyl acetate (3.1.1.1)	*Es*	3	B
General protein	*Pr*	1	B
Glucose phosphate isomerase (5.3.1.9)	*Gpi*	1	B
Glyceraldehyde-3-phosphate dehydrogenase (1.2.1.12)	*Gapd*	1	A
Lactate dehydrogenase (1.1.1.27)	*Ldh*	2	A
Malate dehydrogenase (1.1.1.37)	*Mdh*	2	B
Phosphoglucomutase (2.7.5.1)	*Pgm*	2	B
6-Phosphogluconate dehydrogenase (1.1.1.44)	*6pgd*	1	B
Superoxide dismutase (1.15.1.1)	*Sod*	1	A

* Electrophoretic conditions: A = tris borate EDTA buffer, pH 8.6, 250 volts, 4 hrs; B = tris citrate buffer, pH 6.7, 159 v, 4 hrs.

locus ($\bar{A}$), proportion of polymorphic loci (P), and mean individual heterozygosity by direct count ($\bar{H}$). We performed χ^2 goodness-of-fit tests and also calculated exact probabilities to test for random mating. Wright's (1978) F-statistics were used to assess the extent of genetic differentiation within and between samples and also to test for panmixia. Nei's (1978) unbiased measures of genetic identity (I) and genetic distance (D) were calculated for all pairwise comparisons of samples.

V. Covariance at Level One: The General Pattern

In Figure 5, we plot the loadings of all 55 modern samples (excluding only the six fossil samples) on the first three axes (93.7% of all information) of a varimax rotation for a factor analysis of the matrix of mean vectors. (In this triangular plot, the three loadings for each sample are normalized to a sum of 1.0, thus providing a representation of three dimensions in two, with axes at each corner of the triangle. All but one sample have communalities above 0.87, and this procedure introduces very little distortion of relationships among samples. The strongly dwarfed tapering sample from Sand Cay is the sole exception, with a communality of 0.36; nearly all its remaining information lies on a fourth axis defining it alone.)

The evident order of morphological distribution among samples emerges as a pleasing first result; the lack of pattern in existing taxonomies is, as we had predicted and as we have found in all our *Cerion* work elsewhere, an artifact of definition. The three axes are foci for the three major kinds of *Cerion* on the Turks and Caicos—the indigenous tapering morphotype and the two localized immigrants, *C. blandi* and *C. lewisi*. The most distinctive form, pencil-thin and strongly mottled *C. lewisi*, defines the second axis, and all its samples cluster in a small space of high values. The first axis is a referent for tapering samples, and we can already discern clear order in geographic clustering among islands (discussed fully in the next section on the morphospace of tapering samples alone). In particular, all samples from South Caicos occupy a small, unique field nearest the first axis. *C. blandi* occupies a broader field, high on the third axis, overlapping slightly with samples of the tapering morphotype (with which it hybridizes).

The matrix of factor scores (Table 3) defines the bases for distinctions on these axes. When we consider such covariances for a matrix of samples from a single morphotype generated by a single pattern of growth (see next section), then associations of variables tend to record pathways and constraints of development, and factor

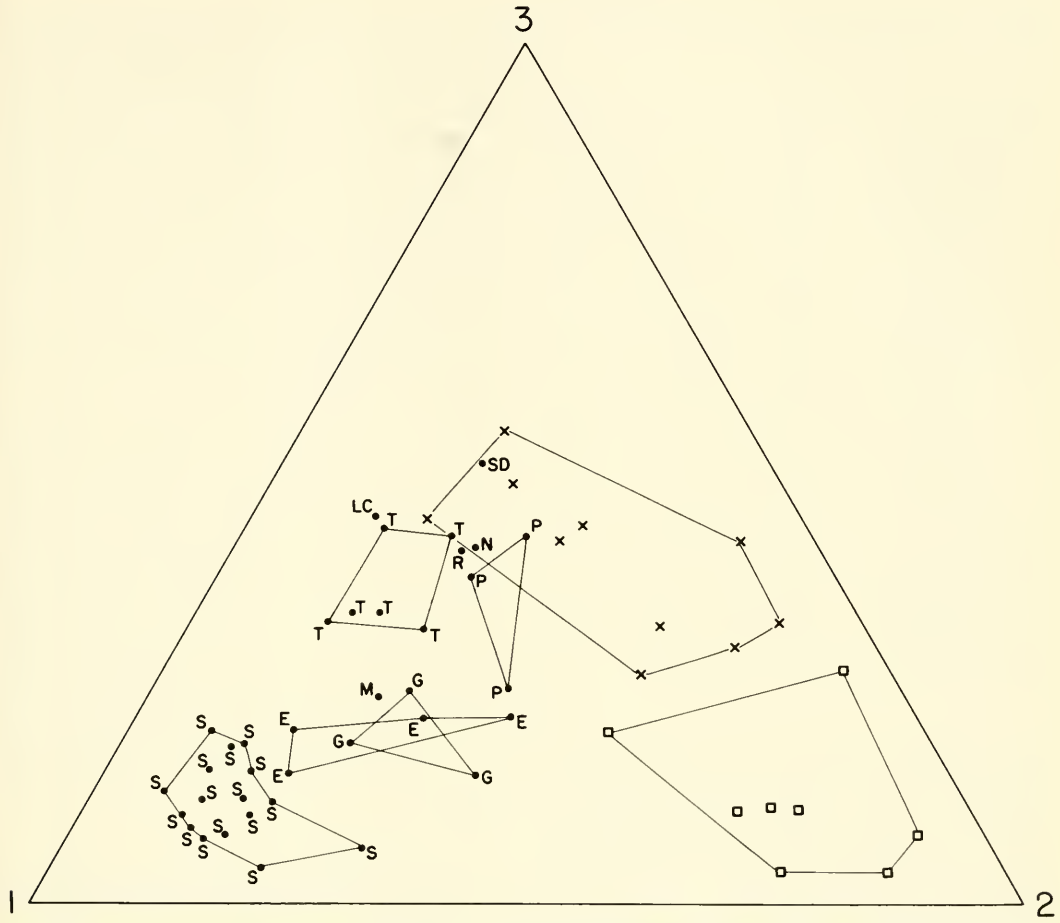


Figure 5. Normalized factor loadings of mean vectors for all nonfossil samples upon the first three varimax axes. Crosses are *C. blandi*, squares *C. lewisi*, and dots *C. regina*. Island for *C. regina* identified as: S, South Caicos; E, East Caicos; M, "Middle" Caicos; N, North Caicos; G, Grand Caicos; P, Providenciales; T, Grand Turk; LC, Long Cay of Turks Bank; SD, Sand Cay of Turks Bank; R, island unknown. Convex polygons are drawn around all samples of *C. lewisi*, *C. blandi*, and *C. regina* from South Caicos, East Caicos, Grand Caicos, Providenciales, and Grand Turk.

analysis becomes a chief tool in the inductive study of constraints and adaptation. But variation lies at too high a level for such an interpretation here because the differences "picked out" by the axes are not dimensions of growth within a coherent form, but the differentia of taxonomic entities forced into the same analysis only by historical contingencies of immigration. Thus, the factor scores of this analysis are records of the basic morphological separation among taxa haphazardly assembled by nature.

The high scores on the second axis all record the chief distinguishing features of its focal cluster, *C. lewisi*—the coordinated characters of a very slender shell achieved by growing many whorls of normal size, not by whorls of unusual height. The shell begins high (0.349 for protoconch height), but height of later whorls do not score strongly. The most distinctive character of slimness (height/width of adult shell at 0.569) is achieved by growing a large number of whorls (0.413), an efficient path to relative narrowness since

TABLE 3. FACTOR SCORES FOR THREE-AXIS SOLUTION (93.7% OF INFORMATION) FOR ALL NONFOSSIL SAMPLES.

Measure	Axis 1	Axis 2	Axis 3
1. PROWID	0.124	0.076	0.141
2. FOURWID	0.269	−0.157	0.265
3. NUMWHO	0.055	0.413	−0.048
4. RIBDENS	−0.093	0.407	0.105
5. LENGTH	0.182	0.233	0.056
6. WIDTH	0.211	−0.079	0.229
7. PROHT	−0.294	0.349	0.493
8. FOURHT	−0.058	−0.030	0.489
9. FRSXHT	0.282	−0.061	0.191
10. UMBWID	0.119	−0.050	0.391
11. LIPWID	0.177	0.046	0.074
12. LIPTHK	0.249	0.020	−0.059
13. APHT	0.230	0.040	0.059
14. APWID	0.253	−0.013	0.037
15. APROT	0.143	0.067	0.129
16. EC	0.236	0.135	−0.022
17. FA	0.171	0.273	0.051
18. APTILT	0.084	0.092	0.032
19. WEIGHT	0.138	−0.027	0.178
20. HWRATIO	0.030	0.569	−0.212
21. PRORAT	0.414	0.086	−0.222
22. FOURRAT	0.353	−0.051	−0.097

the standard allometry of *Cerion* adds height but little or no width throughout middle to late growth (see Gould, 1984b). The numerous fine ribs of this species also distinguish this taxon (0.407) from all other Turks and Caicos *Cerion*.

The third axis, focus for *C. blandi*, records its highest scores for characters well known (see Clench and Aguayo, 1952) as distinct features of its peculiar subgenus *C.* (*Umbonis*)—a wide umbilicus (0.391) and high early heights (0.493 for the protoconch, 0.489 at the end of the fourth whorl). *C.* (*Umbonis*) grows a thin, tapering triangular top by rapid excursion in height, however much the shell may broaden out later in ontogeny.

Scores on the first axis, focus for tapering samples, are more complex because they record two distinct sources of variation—first, a basis of separation between tapering samples and the other two taxa; and, second, the major source of geographic division within tapering samples (note the contrast of South Caicos samples with all others). For the first source, tapering samples are most evidently distinct from other taxa by their generally larger shell size. We find this size difference recorded in the usual manner of factor analytic studies (see Jolicoeur, 1963, 1984)—fairly low and uniform values (averaging about 0.2 in this case) for all measures of basic dimensions in the adult shell (length, width, aperture length and width, sizes of last whorls, that is, measures 5, 6 and 13–17). Standardized sizes of late whorls (fourth width at 0.269, and fourth to sixth height at 0.282) also covary with final sizes.

However, since South Caicos samples load most highly on this axis, we find in addition to these low and uniform scores for general size a few higher scores for distinctive South Caicos characters (see next section), particularly the high values (0.414 and 0.353) for early shell shape (width/height ratios of protoconch and fourth whorl). The relatively flat apices (rapid early growth in width unmatched by height) of South Caicos tapering samples are their chief distinguishing character, both visually and biometrically (see appendix).

VI. Genetics and Morphometrics at Level Two: A Taxonomic Resolution of the Tapering Morphotype

A) The General Pattern: Resolution of Outliers

Figure 6 is a triangular plot of mean vectors for tapering samples alone in their own morphospace. Each island occupies a restricted field arrayed between the first two axes, thus affirming the most important conclusion that we have reached, in study after study, of geographic variation within *Cerion* taxa (Gould, 1984a; Gould and Woodruff, 1978 for example): geographic coherence of shell form marks all *Cerion* distributions; the signature of places is never obliterated.

The array contains an outlier, the strongly dwarfed population from Sand Cay, Turks Bank. Its distinctness is exag-

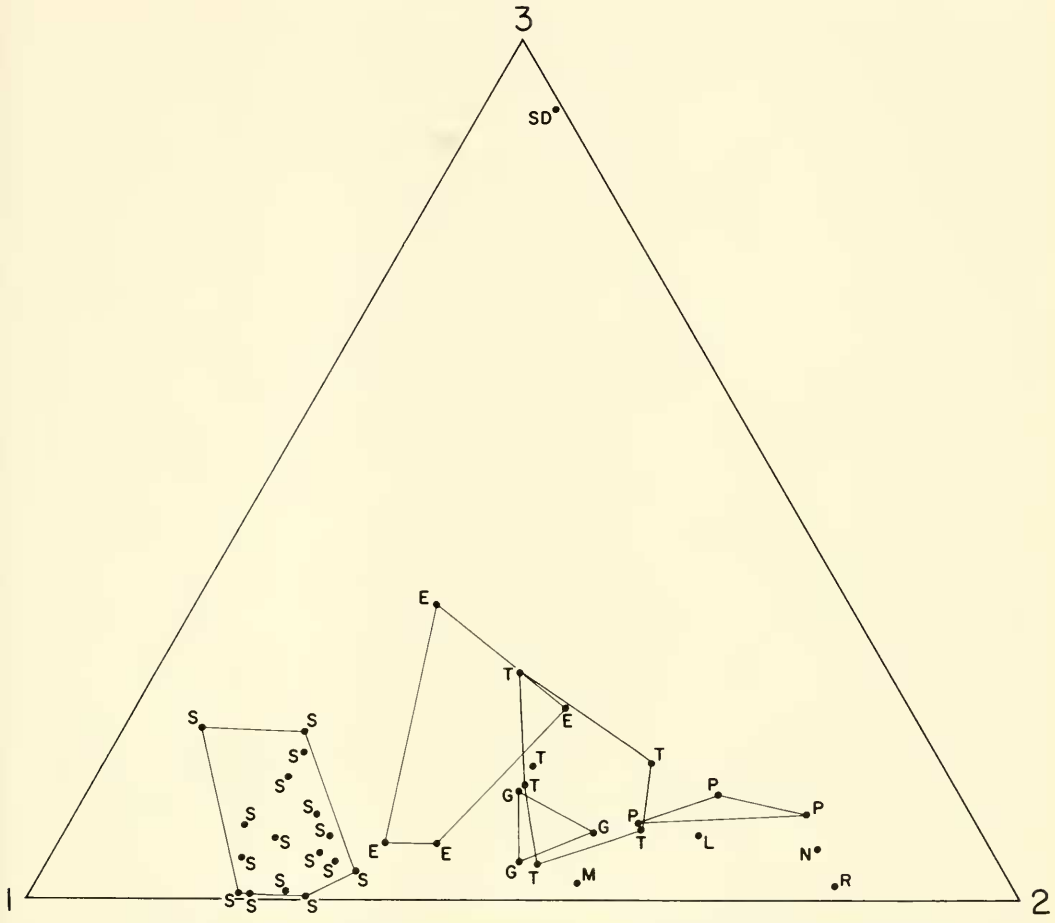


Figure 6. Normalized factor loadings for *C. regina* samples only. Symbols as in Figure 5.

gerated in Figure 6 because factor analysis in varimax rotation tends to absorb uniquenesses on separate axes. The distinctive features of Sand Cay are abstracted by this axis; when plotted into morphospaces that do not include this dimension (as in Fig. 1), Sand Cay plots near all other populations of the tapering morphotype on Turks Bank.

The designation of Sand Cay's uniqueness by an entire axis compresses all other variation into the smaller space of two dimensions. Thus, to expand the portrayal of normal-sized samples in the tapering morphotype, we eliminated the Sand Cay population and repeated the analysis, plotting the triangular diagram as Figure 7. Note that the ordering of normal-sized samples is thereby spread out, but not in any way altered (compare Figs. 6 and 7). The basically linear array of South Caicos-East Caicos-Grand Caicos-Providenciales remains. This array is compressed into two axes on Figure 6, but expanded to three in Figure 7, as the sequence remains fixed in second axis projections, while *each island* now spreads out along the domains of axis one and three.

The Sand Cay population bears, by Clench's own decision (as curator of Mollusks at the Museum of Comparative Zoology), the name *C. utowana abbotti*, one

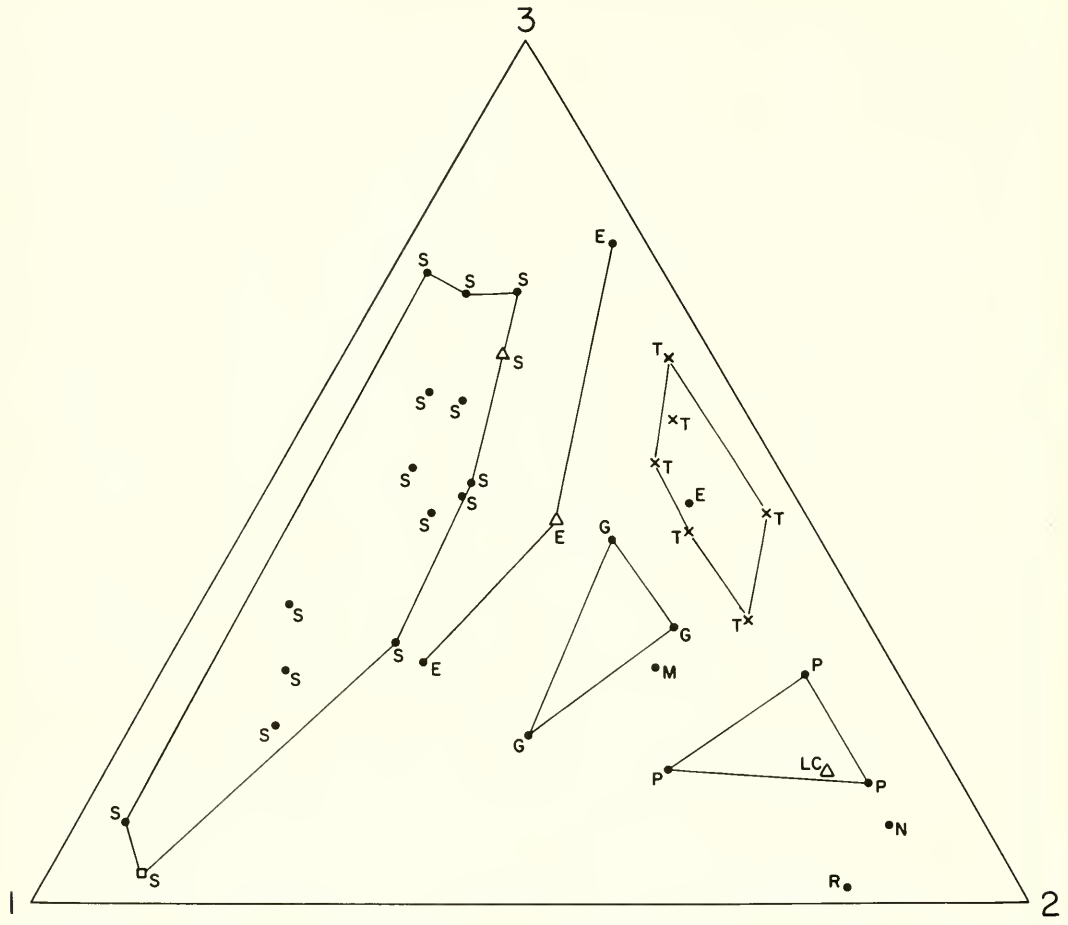


Figure 7. Normalized factor loadings for all *C. regina* samples excluding the Sand Cay dwarfs. Open triangles are samples designated *C. utowana abbotti* by Clench. The open square is the paratype sample of *C. caicosense*.

of the disputed taxa within the tapering morphotype—so one might suspect the validity of this taxon on morphological grounds. But three other samples designated by Clench as *C. utowana abbotti*, including the paratypes from South Caicos, plot (as we shall discuss in part C of this section) at expected positions for their islands within the tapering morphospace. Sand Cay's uniqueness is a consequence of its dwarfing—a simple alteration that provokes, via *Cerion*'s allometries, a large suite of complex changes producing a large overall excursion for the morphological vector considered in toto (see Gould, 1984b; Gould and Woodruff, 1986 for other morphometric analyses of dwarfing in *Cerion*).

The Sand Cay population is not the only strongly dwarfed sample of the tapering morphotype. A subfossil sample from South Caicos (765) yields an even more distant outlier attributable to dwarfing; (see Fig. 8 on the representation of all samples, including the subfossils. Note that axes two and three are reversed relative to Fig. 5, but that the ordering of samples and clusters is not altered). Note that the subfossil

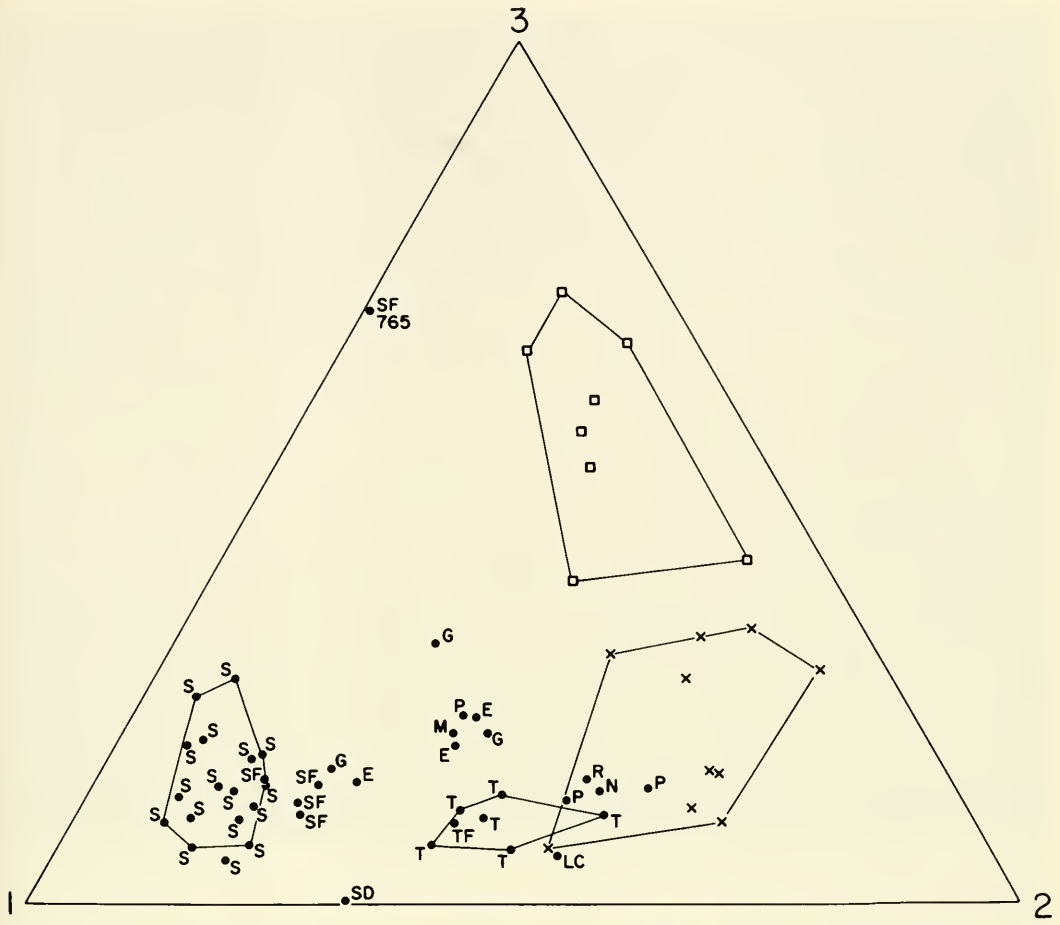


Figure 8. Normalized factor loadings for all samples, now including fossils. Symbols as on Figure 5 with the following additions for fossils. SF, South Caicos fossils (note their position adjacent to but outside the polygon of modern South Caicos samples); TF, Grand Turk fossils; and SF765, smokestack dwarf fossils from South Caicos.

and Sand Cay dwarfs occupy outlying positions at the *opposite* ends of third axis projections.

Fortunately, as the result of a prior study in *Cerion*'s dwarfing (Gould, 1984b), we can identify the common basis in growth and allometry of these apparently contradictory morphological excursions in the two dwarfed populations (see Gould, 1984b). Axis three is the focus in Figure 8 for pencil-thin *Cerion lewisi*. The subfossil dwarfs, projecting as strongly on the third axis as any *C. lewisi* sample, are verging towards "smokestacks" in the terminology of Gould (1984b)—that is, they become dwarfed by restricting whorl size while growing a normal number of whorls. Since *Cerion* increases in height but not in width as later whorls are deposited, this style of dwarfing adds height for a usual amount of coiling to the narrow base of dwarfed whorl size, producing a slender shell. But the Sand Cay dwarfs are "double whammies"—that is, dwarfs through the twin action of reduced whorl size *and* decreased whorl number, leading to squatter than average

Figure 9. Two distinct styles of dwarfing in *C. regina*, producing the major outliers in this species. Left: two specimens from sample 765, South Caicos. Note relative thinning of these smokestack dwarfs with respect to the normal (central) specimen from sample 756, South Caicos. Right: two specimens of Sand Cay dwarfs. Note relatively squatter shells of these "double whammy" dwarfs compared with normal specimen. Leftmost dwarf is 19.1 mm high. Central specimen is 34.9 mm high.

shells through the suppression of whorls that would add height without width. They therefore plot at the opposite end of axis 3, the focus for high-spired *C. lewisi*. This structural understanding of dwarfing and its allometries resolves two issues: first, we can interpret two apparently opposite directions of morphological change as different consequences of the same triggering phenomenon; second, we can accommodate two outlying samples as resolvable expressions of the tapering morphotype, not as taxonomic anomalies. Figure 9 portrays the unusual morphologies of the two dwarfs. Note also (see appendix for more details), the key mean values in the two dwarfed samples for this interpretation. The subfossil smokestack has (at 2.70) the third largest height/width ratio among South Caicos samples, and (at 7.2) a mean whorl number only slightly below average. The Sand Cay "double whammy" has (at 2.20) by far the squattest shell of Turks Island forms, and (at 6.6) by far the smallest number of whorls.

B) Covariances of the Tapering Morphospace

The three axes of Figure 7 include 91.5% of all information, distributed as 25.6 on axis 1, 30.1 on axis 2, and 35.8 on axis 3. Table 4 presents the matrix of factor scores

for projections of variables upon these axes; we shall discuss the associations by decreasing information content of axes.

We recognize the third axis covariance from its similar expression in Table 3. The roughly equal projections for basic dimensions of the adult shell identify this axis as an expression of overall shell size (in Table 3, standardized whorl sizes covary with the raw measures of final size. Here they do not, reflecting the more common pattern of non-association between these two sets in *Cerion*).

Loadings of samples upon the third axis (Fig. 7) affirm this interpretation. This axis makes little distinction among islands, as each island harbors populations spanning a broad range of size. (Lability in size is characteristic of *Cerion*. All previous authors who sought biogeographic pattern with standard techniques of uni- and bivariate biometry were misled, by the large range of size *within* each region, to affirm a lack of distinctness between regions (see, for example, Hummelinck, 1940 and DeVries, 1974 on *C. uva*, corrected by Gould, 1984a. Multivariate techniques have revealed the basis in covariance sets for regional differences easily obscured by large variation in shell size). South Caicos samples, for example, span the entire range of third axis loadings. The generally larger shells of Grand Turk (45–100th percentile among all samples for length, and 51–86th for width) are distinguished by their higher loadings from the smaller shells of Providenciales (20–53rd percentile for length, 15–44th for width).

The second axis is crucial to our interpretation of the tapering morphotype, because it arrays each island in its own subfield, while ordering the Caicos islands in proper geographic sequence (see next subsection where we use this fact as the key for our taxonomic conclusion). Its covariances (Table 4) record a single and sensible pattern. Standardized whorl sizes are all prominent with heights for protoconch and fourth whorl (0.519 and 0.514) greater than widths (0.398 and 0.207). The only other strong values are for height/width ratio of the adult shell (a consequence of growing whorls higher than wide), and for ribs on the first whorl, a correlation that we have never before detected in *Cerion*. Note that this association records but one of the two major developmental pathways to slender shells—the other, and much more common, being simple addition of whorls (as discussed on p. 335). Samples from Providenciales load highest on this axis, South Caicos lowest. The percentile ranges of key variables fit this interpretation. Providenciales samples lie well above average in height/width ratio (64–84th percentile), but *below* in whorl number (27–34th percentile), indicating that relatively slender shells arise by growing high, not more, whorls.

The first axis records no major separation among islands. All high values are for South Caicos samples, but others from this island share lower values with populations from other islands. Turks Island samples are consistently low. The covariance ex-

TABLE 4. MATRIX OF FACTOR SCORES FOR THREE-AXIS SOLUTION OF ALL *C. REGINA* SAMPLES EXCLUDING THE SAND CAY DWARFS.

Measure	Axis 1	Axis 2	Axis 3
1. PROWID	−0.029	0.398	−0.053
2. FOURWID	0.005	0.207	0.173
3. NUMWHO	−0.002	0.046	0.244
4. RIBDENS	0.092	0.267	0.016
5. LENGTH	−0.071	0.093	0.334
6. WIDTH	−0.059	0.062	0.321
7. PROHT	−0.144	0.519	−0.056
8. FOURHT	−0.008	0.514	−0.140
9. FRSXHT	0.307	0.096	0.051
10. UMBWID	−0.070	0.021	0.372
11. LIPWID	0.069	0.044	0.162
12. LIPTHK	0.136	0.025	0.163
13. APHT	−0.053	0.013	0.328
14. APWID	−0.010	0.005	0.286
15. APROT	−0.023	0.043	0.341
16. EC	0.084	0.038	0.210
17. FA	0.391	0.188	−0.084
18. APTILT	−0.058	−0.016	0.249
19. WEIGHT	0.175	0.161	0.118
20. HWRATIO	0.352	0.237	−0.022
21. PRORAT	0.644	−0.156	−0.021
22. FOURRAT	0.321	−0.145	0.207

pressed in factor scores records a fundamental rule of *Cerion*'s growth, but one that we have not detected so clearly in our studies of northern Bahamian *Cerion*.

Consider the pattern in factor scores. Shells begin with low protoconch heights and average widths, yielding a relatively flat nucleus (width/height ratio of the protoconch scores maximally at 0.644). As the shell approaches middle growth, superficial expectations are subverted. Despite the initial advantage in width (still maintained at the fourth whorl, with width/height ratio scoring at 0.321), height asserts itself more and more prominently as the shell grows. Note the continual increase in scores for successive heights: −0.144 for the protoconch, −0.008 for the fourth whorl, and 0.307 for fourth-sixth whorl height. Thus, *early* widths are correlated with *later* heights (not later widths); or, in other words (and now interpreting), shells that begin quite flat compensate later by speeding up growth in height, and height compensation increases continually during middle growth.

We have noted this correlation of early widths with later heights again and again in our studies of land shells, not only in *Cerion* (Gould and Woodruff, 1978, 1986), but also in *Poecilozonites* (Gould, 1969b)—but its interpretation as compensation (keeping final dimensions within a limited range) had previously eluded us. We detect this pattern now because southern Bahamian *Cerion* should record it better. All *Cerion* with flat tops grow parallel-sided (or even width-*decreasing*) shells later in ontogeny, while shells that begin with a triangular top tend to maintain a gentle increase in width throughout growth. We have called the chief morphotype of the southern Bahamas "tapering" because most populations maintain a basic triangularity throughout growth. Yet the same tapering morphotype also includes the most initially flat-topped and later parallel-sided of all Bahamian *Cerion* (*C. malonei* on Long Island, populations of *C. columna* on Inagua, though the phenomenon reaches its extreme expression in species of the Cuban *C. dimidiatum* complex). This transition from triangular throughout growth to first flat-topped and then parallel-sided represents the range of expression for this first-axis covariance set. (We know, from a hybrid zone in Cuba, that direct transitions along this gradient occur, see Galler and Gould, 1979.) We had not detected this pattern in the northern Bahamas because the basic contrast between ribby and mottled morphotypes in this region expresses only a small segment of this range, while the full spate lies recorded among populations of the tapering morphotype.

We can now understand how this compensatory covariance orders populations of the Turks and Caicos. As with variation in size (third axis), all islands display a large range of loadings upon this axis, and few inter-island distinctions can be made. But Grand Turk samples are distinct in their high protoconchs (low width/height ratio from 2.04–2.33), while South Caicos populations tend to be flat-topped (range of 2.26–2.60, with only 1 sample of 20 below the maximal Grand Turk value of 2.33, and eight of 20 above 2.50). Yet this initial distinction is compensated in later growth as the early flatness of South Caicos shells engenders later exaggeration of height—for the final height/width ratios scarcely differ (range of 2.49–2.63 for Grand Turk and 2.44–2.78 for South Caicos).

C) A Taxonomic Decision: All Tapering Populations Belong to the Single Species, *Cerion regina*

The geographically localized and morphometrically restricted *C. blandi* and *C. lewisi* pose no taxonomic problems. They are distinct, immigrant forms and merit recognition as species (despite the hybridization of *C. blandi* with indigenous tapering populations, a pervasive phenomenon among *Cerion* taxa).

The problem of the Turks and Caicos *Cerion* fauna (both in the existing literature and in our morphometric data) centers upon widely varying populations of

the indigenous tapering morphotype. Can they all be gathered under one species, *C. regina* by priority (and a lovely name as "queen *Cerion*"), or have they differentiated to an extent meriting taxonomic subdivision? Three separate issues confront us: the status of morphometric outliers (the two dwarf samples), the validity of existing names in the literature, and the order and extent of morphometric variation among our measured samples.

We have already shown (see p. 336) that the dwarf samples, although morphometrically distant from the major clusters, are products of single transformations (and their correlated effects) noted again and again in dwarfed *Cerion* populations continuous with, and showing no sign of differentiation from, adjacent populations of normal size (Gould, 1984b; Gould and Woodruff, 1986; Woodruff and Gould, 1980).

Four species names exist in the literature for tapering forms from the Turks and Caicos. Clench (1961) had already synonymized the two Turks Island forms by sinking *C. incanoides* Pilsbry and Vanatta, 1895 into *C. regina* Pilsbry and Vanatta, 1895. We do not challenge this decision.

Do paratype populations of the remaining two species, *C. utowana abbotti* and *C. caicosense*, provide any evidence for valid distinction? *C. utowana abbotti* is easily dismissed by our morphometric evidence. As Figure 7 demonstrates, we include three samples named *C. utowana abbotti* by Clench (who described the taxon in 1961)—one from South Caicos (the paratypes), one from East Caicos and one from Long Cay on the Turks Bank. The South and East Caicos samples plot within the arrays of other samples from their island named *C. caicosense* by Clench. We have no other samples from Long Cay, but Clench's *C. utowana abbotti* lies within the morphospace of *C. caicosense*. We may therefore synonymize *C. utowana abbotti* into whatever status *C. caicosense* deserves.

The paratype sample of *C. caicosense* (Fig. 7) lies at the periphery of the South Caicos array (as formally designated taxa so often do), but clearly not apart from it. This population also has no claim for separation beyond its general membership in the South Caicos field.

We must, finally, consider the tapering morphospace itself (Fig. 7). The main argument for taxonomic distinction would lie in the separation of the South Caicos and Turks Island fields, for these are the type areas of the two available taxa, *C. regina* (Turks Island) and *C. caicosense* (South Caicos). Indeed, in the full morphospace of Figure 5, South Caicos lies as far from Grand Turk as the other legitimate taxa, *C. blandi* and *C. lewisi*, lie from each other.

The key to a proper taxonomy for the tapering morphotype lies in how samples from the other islands fit into the morphospace. If we find clear and separated clusters representing the geographically distinct Turks and Caicos banks, then we might admit the two existing names at some formal level. However, all representations of the morphospaces (Figs. 5–8) show the same pattern: populations from other islands of the Caicos Bank fully and continuously fill in the space between separated South Caicos and Turks Island clusters. We therefore find continuity in morphological distribution over the entire recorded range of the tapering morphotype, and no basis for taxonomic distinctions on this account.

But the pattern of intermediacy also speaks for unification through another aspect of its ordering. Our total array (Figs. 6 and 7) contains multiple samples from four islands of the Caicos Bank—Providenciales (3), Grand Caicos (3), East Caicos (4) and South Caicos (16). A comparison with the geography of islands (Fig. 1) shows that each island occupies a discrete part of the morphospace and, more importantly, that the four domains are arrayed in perfect geographical order from South Caicos through East and Grand to the most distant Providenciales (see Fig. 10). Moreover, the equally restricted mor-

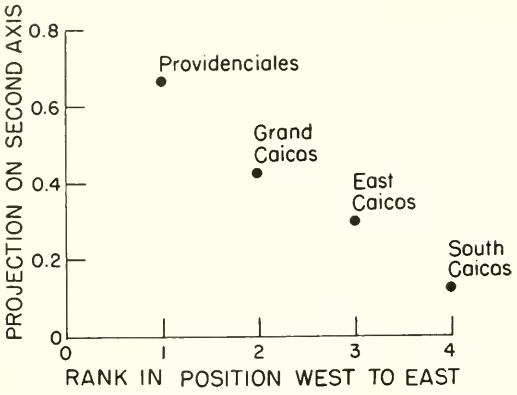


Figure 10. Plot of average projection of all samples upon the second axis versus rank in position along the north edge of the Caicos Bank, west to east.

phological domain of Grand Turk lies within this array.

We also know the basis in covariance for this clinal distribution (see last subsection): an increase in size of standardized early whorls towards Providenciales, with height increasing more than width, leading from the relatively flat-topped populations of South Caicos to the more slender and larger-whorled populations of Providenciales (see Fig. 3). This cline (Fig. 10) records standardized whorl sizes and their consequences for shape, not adult shell size; the Providenciales samples are, if anything, slightly smaller in size than most South Caicos populations, while each island forms a large and nondistinctive array for overall size (Grand Turk shells tend to be large, but one sample lies below the percentile means for adult length and height among tapering samples). All Caicos samples are therefore ordered by geography in a cline defined by a sensible determinant of shape and its associated covariances.

We used the same criterion of geographically ordered clinal distribution in morphology to unite a set of morphologically and geographically more distinct populations into the single species *C. striatellum* from Hispaniola to the Virgin Islands (Gould and Paull, 1977). For all these reasons, we find no basis for any taxonomic distinctions within the tapering morphotype of the Turks and Caicos islands. We therefore synonymize all previous taxa, and recognize only *C. regina* as the appropriate name for the indigenous *Cerion* of the Turks and Caicos islands. The *Cerion* fauna of this geographic outlier of the southern Bahamas therefore includes three species, the native *C. regina* from all major islands, and two restricted immigrants, *C. blandi* from Salt Cay, Turks Bank, and *C. lewisi* from several islands on the northwestern Caicos Bank. The indigenous species belongs to the common morphotype of its general region, while the two immigrants, both fortunately quite distinctive in morphology, have recognizable sources on nearby Cuba.

D) Genetics

This taxonomic conclusion, based solely on conchological and biogeographic data, is strongly supported by our population genetic survey. Although we cannot assess the genetic status of *C. blandi* and *C. lewisi*, we can document the strong genetic relatedness of *C. regina* from Providenciales and South Caicos on the Caicos Bank and Grand Turk on the Turks Bank.

Eight of the 16 genetically interpretable loci were monomorphic in the 17 samples studied: *Crp*, *Es-1*, *Es-6*, *Ldh-2*, *Mdh-2*, *Pgm-1*, *Pr-1*, *Sod-1*. The frequency of the various alleles at the seven polymorphic loci are shown in Tables 5–7. Three loci were diallelic (*Gapd*, *Gpi*, *Pgm-2*); *6Pgd* had three alleles, and three loci had up to four alleles segregating (*Es-2*, *Aat*, and *Mdh-1*). Data for acid and alkaline phosphatases are not reported as the results were uninterpretable. *Ldh-1* data are excluded as only three samples (758–760) were studied; they share a common allele, a second allele was segregating at 759–760, and a third allele was detected at 760.

Tables 5–7 show that the Grand Turk sample (766) is strikingly different from the others in its level of genetic variability. In contrast to the moderate levels of variation seen in all Caicos Bank samples the

TABLE 5. VARIATION IN ASPARTATE AMINOTRANSFERASE AND ESTERASE-2 ALLELE FREQUENCY.

Sample	$\bar{N}$*	$Aat^{1.2}$	$Aat^{1.0}$	$Aat^{0.7}$	$Aat^{0.4}$	$Es\text{-}2^{1.2}$	$Es\text{-}2^{1.1}$	$Es\text{-}2^{1.0}$	$Es\text{-}2^{0.9}$
					Providenciales				
770	29	0.05	0.95	—	—	—	—	1.00	—
772	31	0.00	1.00	—	—	—	0.03	0.97	—
					South Caicos				
753	32	0.03	0.97	—	—	—	—	1.00	—
757	29	0.10	0.90	—	—	—	—	1.00	—
754	32	0.03	0.97	—	—	—	—	1.00	—
758T	23	0.04	0.96	—	—	—	—	1.00	—
758	32	0.10	0.90	—	—	—	—	1.00	—
759	29	0.07	0.91	—	0.02	—	—	1.00	—
760	31	—	1.00	—	—	—	—	1.00	—
761	29	—	1.00	—	—	—	—	1.00	—
762	32	—	1.00	—	—	—	0.03	0.97	—
764	31	—	0.98	0.02	—	0.02	0.02	0.96	—
749	32	—	1.00	—	—	—	—	0.94	0.06
750	32	—	0.94	0.06	—	—	—	0.98	0.02
751	32	—	0.97	0.03	—	—	—	1.00	—
752	32	—	1.00	—	—	—	—	0.98	0.02
					Grand Turk				
766	31	—	1.00	—	—	—	—	1.00	—

* $\bar{N}$ = mean sample size per locus.

31 snails from Grand Turk were isogenic at all loci studied. However, as the Grand Turk sample is fixed for the common allele segregating at each polymorphic locus on South Caicos it is clearly closely related to the Caicos populations. We hypothesize that the Turks Island populations are descendants of a very few colonists from the Caicos Bank that, by chance, failed to carry or subsequently lost, the less frequent alleles of the source population. Such a scenario is in keeping with the traditional view that much interisland dispersal of *Cerion* results from the vagaries of hurricane transportation. At least one other species, *C. incanum*, is known to be isogenic in part of its range (Woodruff and Gould, 1987). In the lower Florida Keys four samples of 30 snails each were all monomorphic at 17 loci. One hundred km further north at Key Biscayne adjacent to the Florida mainland three samples showed variation at 1–2 loci.

The variation in allele frequencies reported in Tables 5–7 were used to establish the mating system and population structure of *C. regina*. The allele frequency estimates are reasonably robust as sample sizes were typically more than 30 individuals. A measure of the replicability of these estimates is provided by the comparison of data for samples 758T and 758; allele frequency differences at the three polymorphic loci (*Aat*, *Mdh-1*, *6Pgd*) are insignificant. (Note also that both samples were treated morphologically and found indistinguishable, see Figs. 14, 16.)

We tested genotype frequency data for each variable locus in each sample for significant deviation from values expected under panmixia. In only three of 67 χ^2-tests did the probability that the frequencies were in Hardy-Weinberg equilibrium fall below 0.05. In these cases, however, the simple χ^2-tests were inappropriate and when exact probabilities were calculated these were all >0.15. We conclude that *C. regina*, an anatomical hermaphrodite, is outbreeding at random on Providenciales and South Caicos. This conclusion was supported by the calculation of Wright's index, F_{is}, the inbreeding coefficient of an

TABLE 6. VARIATION IN GLUCOSE PHOSPHATE ISOMERASE, GLYCERALDEHYDE DEHYDROGENASE AND MALATE DEHYDROGENASE-1 ALLELE FREQUENCY.

Sample	$Gpi^{1.4}$	$Gpi^{1.0}$	$Gapd^{1.0}$	$Gapd^{0.7}$	$Mdh\text{-}1^{1.2}$	$Mdh\text{-}1^{1.0}$	$Mdh\text{-}1^{0.8}$	$Mdh\text{-}1^{0.6}$
				Providenciales				
770	—	1.00	0.97	0.03	0.02	0.69	0.03	0.26
772	0.03	0.97	1.00	—	—	0.84	—	0.16
				South Caicos				
753	—	1.00	0.95	0.05	0.02	0.76	0.02	0.20
757	—	1.00	1.00	—	—	0.62	—	0.38
754	—	1.00	1.00	—	—	0.72	0.02	0.26
758T	—	1.00	1.00	—	—	0.50	—	0.50
758	—	1.00	1.00	—	—	0.47	0.03	0.50
759	0.02	0.98	1.00	—	0.04	0.60	0.04	0.32
760	0.02	0.98	1.00	—	—	0.58	—	0.42
761	—	1.00	1.00	—	—	0.68	0.02	0.30
762	0.02	0.98	1.00	—	—	0.91	—	0.09
764	0.02	0.98	1.00	—	—	0.94	—	0.06
749	—	1.00	0.92	0.08	—	0.83	0.14	0.03
750	0.03	0.97	0.86	0.14	—	0.92	—	0.08
751	0.02	0.98	0.94	0.06	—	0.88	—	0.12
752	0.02	0.98	0.86	0.14	—	0.72	—	0.28
				Grand Turk				
766	—	1.00	1.00	—	—	1.00	—	—

individual relative to its sample. The mean F_{is} for all seven polymorphic loci in all samples was 0.036 indicating that the snails sampled could all have been drawn from a single outbreeding metapopulation. Finally, we calculated coefficients of heterozygote deficiency for all variable loci and again found no significant heterozygote deficiency or excess in the samples. All three approaches indicate that *C. regina* is amphimictic on the Caicos Bank.

These tests cannot, of course, be applied to the monomorphic snails of Grand Turk (sample 766). It seems most unlikely that their isogenicity is due to a radical change in reproductive strategy—from outbreeding to self-fertilization—as the ability to do so is unknown in *Cerion*. Instead, as hypothesized herein, we attribute their genetics to a founder effect associated with the successful colonization of the Turks Bank by a few snails from the Caicos Bank. The study of additional samples from this, the most isolated of the Bahamian banks, should clarify this situation.

The remaining 16 samples representing 15 populations from Providenciales and South Caicos on the Caicos Bank are all moderately variable (Tables 5–7). The mean number of alleles per locus $\bar{A} = 1.3$ (range 1.2–1.5), the mean proportion of polymorphic loci $\bar{P} = 0.28$ (range 0.20–0.40), and the mean individual heterozygosity $\bar{H} = 0.06$ (range 0.05–0.09). The typical sample is thus polymorphic at four of the 15 loci and the most variable sample (750) at six loci. These levels of intrapopulation variability in *C. regina* are very similar to those determined for other well-characterized species of *Cerion* (Gould and Woodruff, 1978, 1986; Woodruff, 1975; Woodruff and Gould, 1987). Although these estimates of genetic variation are minimum estimates (as they are based on single-gel electrophoresis) they probably reflect 80% of the true variation at these structural gene loci (Ayala, 1983; Selander and Whittam, 1983).

The finding that *C. regina* is amphimictic permits us to use Nei's (1978) unbiased measures of multilocus genetic identity (I) and genetic distance (D) to

TABLE 7. VARIATION IN PHOSPHOGLUCOMUTASE-2 AND 6-PHOSPHOGLUCONATE DEHYDROGENASE ALLELE FREQUENCY AND IN OVERALL SAMPLE GENETIC VARIABILITY.

Sample	*Pgm-2*$^{1.3}$	*Pgm-2*$^{1.2}$	*6Pgd*$^{1.0}$	*6Pgd*$^{0.9}$	*6Pgd*$^{0.8}$	$\bar{A}$	*P*	$\bar{H}$
				Providenciales				
770	0.02	0.98	0.79	0.21	—	1.5	0.33	0.06
772	—	1.00	0.69	0.29	0.02	1.3	0.27	0.06
				South Caicos				
753	0.02	0.98	0.80	0.20	—	1.5	0.33	0.05
757	—	1.00	0.83	0.17	—	1.2	0.20	0.06
754	—	1.00	0.76	0.24	—	1.3	0.20	0.05
758T	—	1.00	0.68	0.32	—	1.2	0.20	0.06
758	—	1.00	0.59	0.41	—	1.3	0.20	0.09
759	0.02	0.98	0.64	0.36	—	1.5	0.33	0.08
760	0.02	0.98	0.71	0.29	—	1.3	0.27	0.07
761	0.02	0.98	0.76	0.24	—	1.3	0.20	0.05
762	—	1.00	0.56	0.39	0.05	1.3	0.27	0.05
764	—	1.00	0.55	0.43	0.02	1.5	0.33	0.05
749	—	1.00	0.84	0.16	—	1.3	0.27	0.05
750	—	1.00	0.69	0.31	—	1.4	0.40	0.06
751	—	1.00	0.66	0.34	—	1.3	0.33	0.06
752	—	1.00	0.60	0.40	—	1.3	0.33	0.08
				Grand Turk				
766	—	1.00	1.00	—	—	1.0	0.0	0.0

$\bar{A}$ = mean no. alleles per locus, *P* = proportion of loci polymorphic, $\bar{H}$ = mean individual heterozygosity per locus.

assess the overall pattern of differentiation within this species. The results show that only minor geographic differentiation has occurred, a finding concordant with the calculation of Wright's fixation index (F_{st} = 0.08). A similarity matrix (available from D.S.W.) for all pairwise comparisons of the 17 samples showed *I* values to range from 1.00 to 0.982 on South Caicos. Overall similarity is higher than this range suggests as 75% of the 136 values ≥0.995. The lowest *I* value (0.971) involved samples 758 (northeast South Caicos) and 766 (Grand Turk).

The similarity matrix can be visualized by cluster analysis. Here we present a genetic distance phenogram (where $D = -\ln I$) prepared by the unweighted pair group with averaging (UPGMA) algorithm (Fig. 11). Nei's genetic distance, *D*, a multilocus measure of intersample differences, may range between 0.00 (identity) and infinity. Within a group of sexually reproducing organisms *D* values increase with taxonomic distance. For example, only about 2% of 7,000 estimates of *D* between conspecific populations of a wide range of organisms exceed 0.10 and only 2% of 900 estimates of *D* between congeneric species fell below 0.15. Interspecific genetic distances of mammals, fish, and reptiles are typically in the range of $D = 0.3–0.5$ (Avise and Aquadro, 1982) and published results for mollusks are also generally in this range (Woodruff and Merenlender, in prep.). *Cerion* (and birds) are a little exceptional in that they show less differentiation within and between species than most other groups. Nevertheless, no *Cerion* species or semispecies are known where the interspecific *D* is less than 0.05 or the intraspecific *D* exceeds a similar value (Gould and Woodruff, 1986; Woodruff and Gould, 1980, 1987).

Given this background it is clear from Figure 11 that *C. regina* is remarkably homogenous genetically. After pairwise averaging, the greatest *D* value separating clusters of samples is only 0.01. It must be remembered that the error on such small

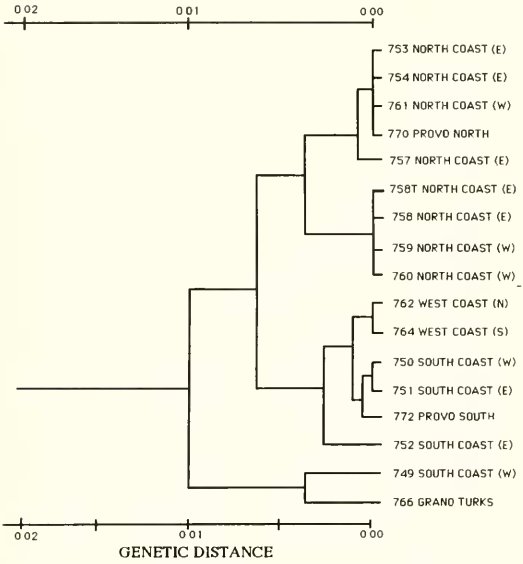


Figure 11. A dendrogram based on UPGMA clustering of 17 samples of *Cerion regina* from Providenciales, South Caicos and Grand Turk using the unbiased genetic distance (*D*) of Nei (1978). Samples are identified according to their locality number and geographic location (*PROVO* = Providenciales; *N*orth, *S*outh, *E*ast, *W*est).

branch-point estimates exceeds the *D* value itself; no great biological significance can be placed on the subclustering in Figure 11. Notwithstanding this caution, we immediately note two interesting aspects of clustering in the 17 samples. The first is that the Providenciales samples are embedded in the South Caicos cluster. Samples 770 and 772 from the north (bank-edge) and south (bank-interior) coasts of Providenciales are genetically indistinguishable from samples from South Caicos. Most interestingly, these two samples cluster with the biogeographically equivalent groups on South Caicos, i.e., 770 with the northeastern bank-edge group, 772 with the southwestern bank-interior group. (This within island patterning will be discussed in more detail in section VII.) The second significant result in Figure 11 involves Grand Turk (766): *Cerion* on this isolated island bank are indistinguishable from those of the Caicos Bank. The only distinction (manifest as $\bar{D} = 0.01$) stems directly from the fact that Grand Turk's snails are fixed for the common alleles on the Caicos Bank. There is thus no genetic evidence to support the recognition of *C. caicosense* as a separate species. Again, no special significance can be placed on specific branch-points at this level of differentiation so the clustering of sample 766 with sample 749 (southwest South Caicos) does not indicate that the Turks Bank populations were founded by this Caicos population. In fact, individual snails homozygous at all variable loci for the same alleles that are fixed on Grand Turk occur in every one of the South Caicos and Providenciales samples.

The genetic data therefore lead to the following conclusions. *C. regina* is a typical amphimictic species. Despite fragmentation of populations today on two island banks separated by the 32 km wide Turks Island Passage there is no evidence of genetic differentiation. Similarly, the populations on Providenciales and South Caicos, presumably continuous a few thousand years ago but separated today by about 100 km of water, are genetically indistinguishable. Such low levels of genetic differentiation are typical of other known species of *Cerion* and of conspecific populations generally.

E) A Note on Minor Axes and General Geometry

We have seen that the major axes of our factor analyses sort the islands into discrete groups and order them into a clinal array that supports the unification of all populations into the single species *Cerion regina*.

We have argued in previous works (Gould and Woodruff, 1978, 1986 in particular) that minor axes should not be ignored, for they may display significant biological information based on few variables in few samples (even if statistically "insignificant" in another, technical sense of the word). In the *C. regina* morphospace, most minor axes yield no general interpretation, for they capture only the peculiarities of

single samples for single measures. But the fourth axis, carrying some 10% of information, displays a coherent and interesting aspect of covariance well known from all our *Cerion* studies. Note, in Table 8, that three of the highest scores form a well-known covariance set based on whorl number and its consequences for shape—many whorls (0.390) produce a high (0.225), not a wide (0.012), shell because later whorls, in the second allometric phase, add height but little or no width, leading to large height/width ratio of the adult shell (0.416).

If we now consider the two highest negative scores, we note standardized whorl sizes of the early shell—fourth whorl width at −0.277 and fourth to sixth whorl height at −0.248. This negative association is the pervasive constraint—we call it the constraint covariance—that we have identified in all *Cerion* studies (see particularly Gould and Paull, 1977; Gould and Woodruff, 1978). If a shell begins by growing larger than average whorls, it will necessarily grow fewer of them to reach the same final size. Thus, when final sizes fall in a limited range, we find negative associations between whorl numbers and measures of standardized whorl sizes. This constraint holds particular interest because it imposes forced correlations for basic shape as well. The shell with small and many whorls will be slender and parallel-sided, while the alternative with fewer, larger whorls will be squatter and continually increasing in width. These forced correlations arise because shells, in the second allometric phase, add height but little or no width. The more whorls added in this phase, the more slender the adult shell (Gould, 1984b).

When we plot (Fig. 12) all samples onto this constraint axis, we note a different pattern. High values do not mark any geographic location, but rather pluck out a sample or two from each major place; the five highest loadings include two for East Caicos and one each for Grand Caicos, Providenciales and Grand Turk. (Two East Caicos samples are high, but the other two from this island are lower than average.) The constraint covariance is a pervasive rule of growth within all *Cerion*, not the unique association of a single place. Thus, it can "attract" samples from any region that happen to grow (in this case) with small whorls, and thereby develop with the forced correlations so implied. Finally, we note in Figure 13 that the constraint covariance acts in the same way upon the full morphospace, selecting one or two samples from all taxa and regions by virtue of smaller than average whorls that can occur in *any* taxon or region, and then carry their train of enjoined consequences with them.

TABLE 8. FACTOR SCORES ON FOURTH AXIS (12.6% OF INFORMATION) OF AN ANALYSIS FOR ALL TAPERING SAMPLES EXCEPT FOR SAND CAY DWARFS.

Measure	Axis 4
1. PROWID	−0.210
2. FOURWID	−0.277
3. NUMWHO	0.390
4. RIBDENS	0.442
5. LENGTH	0.225
6. WIDTH	0.012
7. PROHT	0.164
8. FOURHT	−0.097
9. FRSXHT	−0.248
10. UMBWID	0.204
11. LIPWID	0.138
12. LIPTHK	0.030
13. APHT	0.132
14. APWID	0.099
15. APROT	0.272
16. EC	−0.000
17. FA	−0.108
18. APTILT	0.243
19. WEIGHT	−0.084
20. HWRATIO	0.416
21. PRORAT	−0.115
22. FOURRAT	−0.031

VII. Covariation at Level Three: Does Order Still Reign Within Islands?

Descending now to the finest level of among-sample relationships, we shall consider the distribution of samples for a single island, our most completely collected

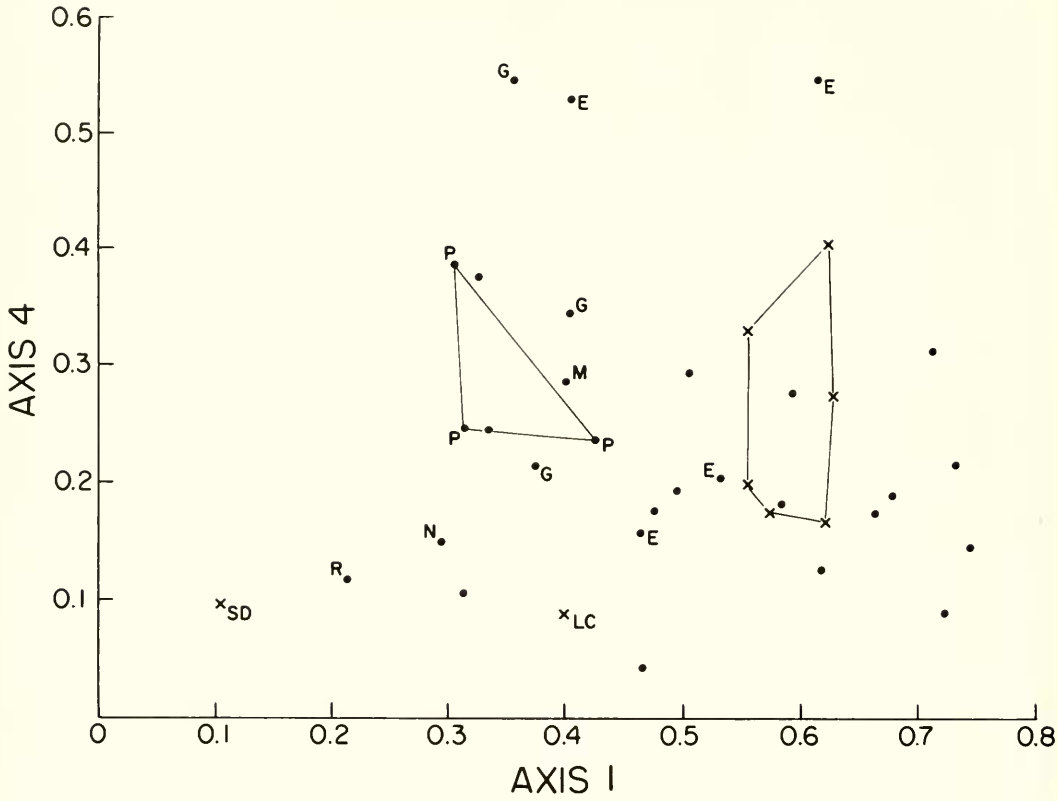


Figure 12. Loadings of mean vectors for *C. regina* samples upon first and fourth axes. Symbols as in Figure 5 except Caicos Bank samples are dots and Turks Bank samples are crosses. Note that the fourth axis, expressing the geometrically necessary negative covariation of whorl size and whorl number, does not identify any particular region, but isolates a few samples from several regions.

South Caicos, within their own morphospace. We have shown (both here and in all our *Cerion* studies of other island groups) that geographic variation *within* islands also displays ordered pattern rather than random arrays. (Thus, older claims for crazy-quilt distributions are false at all levels—from the highest of taxonomic separation between major banks to the finest of minor differentiation within single taxa on single islands.) We have found repeated order based on recurrent habitat (Gould, 1984a on windswept platforms versus secluded valleys, and on limestone or volcanic substrates in *C. uva*), and on simple geographic contiguity [distinction of Treasure Cay samples of *C. bendalli* on Abaco (Gould and Woodruff, 1978); or of offlying cay populations of *C. glans* on New Providence (Gould and Woodruff, 1986)]. We now report a similar coherence for tapering samples on South Caicos as well.

The five-axis solution for South Caicos samples seems to capture all important dimensions of covariance, with no subsequent axis including even one percent of information. We plot, as Figure 14, the loadings of all South Caicos samples (excluding the subfossil dwarf outlier, 765, discussed earlier) upon the two axes explaining most information (axis 1 at 37.9% and 3 at 23.9%; no other axis exceeds 15%). A comparison of these loadings with geo-

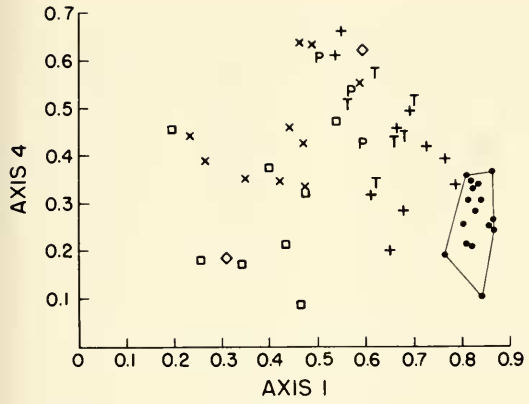


Figure 13. Loadings of mean vectors for all samples upon first and fourth axes. Note, as in Figure 12, that the fourth axis isolates some samples from all regions and taxa. As in Figure 5, crosses are *C. blandi* and squares are *C. lewisi.* For *C. regina* dots are South Caicos; plusses are other Caicos islands; T are Grand Turk; and diamonds are other Turks Bank samples.

graphic position (Fig. 15) shows that samples plot into the South Caicos morphospace largely by geographic location; subregions of this small island can be iden-

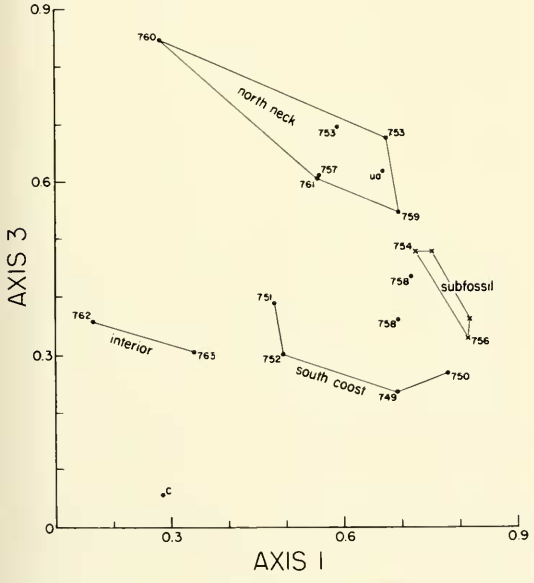


Figure 14. Loadings for South Caicos samples only. Dots are modern samples, crosses are fossils. All points include our collection number (see Fig. 14) except for the two paratype samples collected previously: c is *C. caicosense*; ua is *C. utowana abbotti.* Note good separation by region and time, even on this very small island.

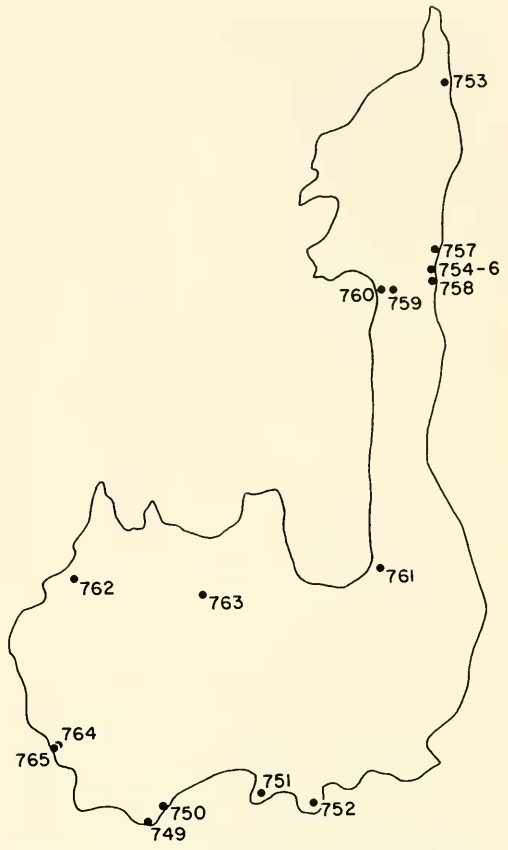


Figure 15. Outline map of South Caicos showing location of our samples.

tified by morphology. In addition, we gain some confidence in our methods of measurement by noting that for two locations with two samples each (753 and 758), the two loadings for each place are adjacent. (In each location, snails in one sample came from a single tree, and the other sample from surrounding grass and bushes.)

The first axis distinguishes subfossil samples by high loadings and the two interior samples (at the airstrip) by low loadings. The third axis contrasts samples from the northern neck of the island (high loadings) with central and southern samples. Taken together, we may identify four broad temporal and geographic domains (not distinct clusters since they overlap, but not random arrays because they do not interpenetrate):

TABLE 9. SCORES OF FIVE-AXIS SOLUTION FOR SOUTH CAICOS SAMPLES.

Measure	Axis 1	Axis 2	Axis 3	Axis 4	Axis 5
1. PROWID	0.331	−0.043	−0.011	0.061	0.156
2. FOURWID	0.260	0.025	0.142	0.155	0.320
3. NUMWHO	0.079	−0.031	0.170	−0.365	−0.133
4. LENGTH	0.226	−0.070	0.096	−0.091	−0.038
5. WIDTH	0.206	−0.114	0.171	−0.031	0.156
6. PROHT	0.380	−0.076	−0.209	−0.286	−0.016
7. FOURHT	0.403	0.473	−0.124	0.306	−0.015
8. FRSXHT	0.341	0.024	0.052	0.233	0.170
9. UMBWID	0.030	0.053	0.427	0.052	−0.047
10. LIPWID	0.240	0.063	0.092	0.078	−0.292
11. LIPTHK	0.167	−0.030	0.066	−0.066	−0.113
12. APHT	0.230	−0.082	0.146	−0.008	−0.044
13. APWID	0.188	−0.096	0.178	−0.046	0.040
14. APROT	0.192	−0.019	0.312	−0.072	−0.214
15. EC	0.122	−0.145	0.014	−0.371	0.229
16. FA	0.056	0.346	−0.255	−0.475	0.391
17. APTILT	−0.108	0.005	0.486	−0.129	−0.126
18. HWRATIO	0.076	0.409	−0.031	−0.397	−0.448
19. PRORAT	−0.209	0.638	0.330	0.066	0.235
20. FOURRAT	−0.094	−0.103	0.308	−0.196	0.416

subfossils (all from the northern neck), modern samples from the northern neck, the south coast, and the western interior at the airstrip. We were surprised (and pleased) to find these distinctions on such a small island with populations in broad contact. The type sample of *C. caicosense*, with high loadings on the second axis (see below), plots with low loadings on both axes of Figure 14.

The patterns of covariance revealed by factor scores help to explain these patterns among samples (Table 9). We recognize, in the nearly uniform scores for all measures of size (final and whorl-standardized in this case) on the first axis (37.9%), the signature of general size that we have identified at all levels in this study. We can therefore identify the basis for distinction of the large subfossils. More important, we now note for the first time in the tapering morphotype the same basic pattern that sets relationships of size in the ribby and mottled morphotypes of the northern Bahamas: large and thick shells of exposed coasts contrasting with smaller and thinner shells of calm coasts and island interiors. Note this contrast for divisions *within* both the southern and northern domains on South Caicos. In the north, the samples of the exposed, bank-edge east coast (753, 758) load high, and the calm, bank-interior west coast low (760). In the south, coastal samples are high (749–752), interior samples low (762–763).

The second axis (14.4% of information), with high loadings only for the *C. caicosense* paratypes and two southern samples (752, 762) expresses an aspect of the central covariance regulating *Cerion*'s shape, and discussed above (p. 337): the play-off between initial flatness and later acceleration in height (leading to an apparent contrast that actually represents two expressions of the same rule at opposite extremes of its action—a shell roughly triangular throughout and continually expanding in width, versus a flat-topped shell compensated later by rapid growth in height to produce a parallel-sided adult shell). *C. caicosense* is, apparently, not a valid taxon, but the name given to one end of this continuity in a key morphogenetic rule—the flattened nucleus and later compensation in height most characteristic of South Caicos' unique samples (see Figs. 5–

8). All high scores on the second axis fit this interpretation [initial flatness (width/height ratio of the protoconch at 0.638), followed by compensatory height (fourth whorl height at 0.473, and last whorl height FA at 0.346), leading to a high-spired shell (final height/width ratio at 0.409)].

The third axis (23.9%), the other major basis of sensible distinctions among South Caicos samples, captures another aspect of this key covariance in shape. Initial flatness, this time of both protoconch (measure 19 at 0.330) and fourth whorl (measure 20 at 0.308), is compensated by continually increasing assertion of standardized height (smooth increase of scores for measures 6–8 from −0.209 to −0.124 to 0.052). In addition (and if related by developmental architecture, we do not know how), we find correlated high scores for the three measures of accentuated change of shape in the adult aperture, the third allometric phase of *Cerion* (apertural rotation, measure 14, at 0.312; apertural tilt, measure 17, at 0.486; and umbilical width, measure 10, increasing as the aperture tilts away, at 0.427). Thus, samples with high loadings on this axis have strong apertures and flattened tops, followed by later compensatory growth in height. This distinction sets the primary contrast between northern and southern samples on South Caicos.

The fourth and fifth axes (14.7 and 6.6% of information) do not make broad geographic distinctions among samples. Both emphasize the standardized sizes of early whorls in their covariances, and we find, as we have before (see Gould and Paull, 1977, for example), a contrast between heights (fourth axis) and widths (fifth axis). Other high scores associate sensibly with these standardized sizes according to the principal constraint that we have identified in *Cerion* (discussed in section VI E): under limitations upon final shell size, large early whorls imply fewer total whorls, leading to forced correlations in final shape, especially the building of greater height along the many and small whorled pathways. Note the negative association of whorl number (−0.365) and final height/width ratio (−0.397) with high scores for standardized heights (0.306 for fourth whorl, 0.233 for fourth to sixth whorl) on axis 4. The same pattern repeats on the fifth axis, where strong standardized widths (0.156 for the protoconch, 0.320 for the fourth whorl) associate negatively with whorl number (−0.133), final height/width ratio (−0.448), and also yield in this case, a flattened top produced by the strong early widths (unmatched by heights): 0.235 for width/height of protoconch, and 0.416 for width/height at the fourth whorl.

The triangular, three axis solution collapses this covariance by amalgamating general size with one aspect of the key shape covariance (the flat-top later-height principle) on the first axis (now 55.8% of information), according (as in the 5-axis solution) another aspect of this key shape covariance to the second axis (now 19.2%), and joining the fourth and fifth axes into a single axis (the third at 17.5%) by incorporating both standardized heights and widths, and recording the chief constraint of negative interaction between large early sizes and few total whorls. These covariances are expressed in Table 10. This arrangement divides the determinants of form within the South Caicos morphospace into its three major principles—size on the first axis, the major covariance determining variation in shape on the second (the compensation of initial flatness by later growth in height), and the major constraint forcing correlations among characters on the third (negative association between whorl size and whorl number under limitations upon the range of final shell size).

The triangular plot of sample loadings (Fig. 16) makes the same distinctions as Figure 14, with tighter clustering around the now more dominant first axis, and greater separation of the *C. caicosense* paratypes on the second axis, and the interior samples (762–763) on the third. This figure also records an important point about

TABLE 10. SCORES OF THREE-AXIS SOLUTION FOR SOUTH CAICOS SAMPLES.

Measure	Axis 1	Axis 2	Axis 3
1. PROWID	0.302	0.097	0.172
2. FOURWID	0.363	0.124	0.183
3. NUMWHO	0.127	−0.061	−0.375
4. LENGTH	0.230	−0.029	−0.063
5. WIDTH	0.315	−0.048	0.005
6. PROHT	0.197	0.129	−0.029
7. FOURHT	0.166	0.527	0.260
8. FRSXHT	0.333	0.126	0.265
9. UMBWID	0.230	−0.098	−0.183
10. LIPWID	0.143	0.007	−0.025
11. LIPTHK	0.140	−0.025	−0.070
12. APHT	0.258	−0.062	−0.019
13. APWID	0.269	−0.071	−0.048
14. APROT	0.261	−0.113	−0.215
15. EC	0.197	0.001	−0.174
16. FA	−0.025	0.543	−0.218
17. APTILT	0.142	−0.202	−0.389
18. HWRATIO	−0.139	0.296	−0.493
19. PRORAT	−0.017	0.444	−0.245
20. FOURRAT	0.229	−0.081	−0.186

taxonomic practice. We see that the invalid names *C. utowana abbotti* and *C. caicosense* are not geographically defined areas of microdifferentiation, but extreme expressions (within the morphospace) of tendencies in covariance common to the entire sample—*C. utowana abbotti* by size, *C. caicosense* by the major shape covariance set.

Thus, variation within South Caicos is both geographically coherent and expressed along the major lines of developmental channeling in *Cerion*—a fine example of the interplay (not antithesis) between themes of constraint and adaptation.

A similar pattern of geographic coherence can be seen in the genetic data for the 13 populations sampled on this small island. Figure 11 clearly shows two clusters of samples: those from the northeast of the island and those from the south and west coasts. (Note that the populations sampled are the same as those discussed morphometrically except for the omission of 763 and the addition of the west coast 764.) Inspection of Tables 5–7 reveals the minor differentiation underlying this dichotomy. The northern end of the island is characterized by higher frequencies of $Aat^{1.2}$, $Mdh\text{-}1^{1.2}$, $Mdh\text{-}1^{0.8}$, $Mdh\text{-}1^{0.6}$ and $Pgm\text{-}2^{1.3}$. The southern and western populations have higher frequencies of $Aat^{0.7}$, $Es\text{-}2^{1.2}$, $Es\text{-}2^{1.1}$, $Es\text{-}2^{0.9}$, $Gpi^{1.4}$, $Gapd^{0.7}$ and $6Pgd^{0.8}$. The allele $6Pgd^{1.0}$ shows apparently clinal variation: decreasing in frequency from 0.8 in the north to about 0.55 in the southwest, with the south coast samples showing intermediate values. The overall pattern of geographic differentiation on South Caicos thus involves all seven polymorphic loci and is remarkably similar to the pattern revealed morphometrically.

Certain parallels can be drawn between the geographic pattern of genetic differentiation seen on South Caicos and that found previously in the northern Bahamas. On New Providence Island, for example, we found two imperfectly isolated species with an interspecific D of about 0.05 (Gould and Woodruff, 1986). The two taxa showed consistent differences in shell morphology and distribution. *C. glans*, typically with unmottled strongly ribbed shells, is restricted to coastal sites within 3–7 km of the edge of the island bank. *C. gubernatorium*, on the other hand, has mottled finely ribbed shells and is found in the interior of the island and on coasts adjacent to the bank interior. It has not been found at the bank edge. Today the two species hybridize and morphological hybrids have been collected over distances of <1 km where the ranges come into contact. Genetic introgression is, however, more extensive: *C. gubernatorium* alleles have swept into the bank-edge coast populations of *C. glans* and *C. glans* alleles have introgressed 3 km beyond the limits of morphological hybridity. Today, we find genetically "pure" *C. gubernatorium* restricted to the southeast corner of this narrow island (average width 7 km) where they are 5–7 km away from the influence of *C. glans*. The genetic hybrid zone on New Providence is an area of genetic anomaly. Hybrid populations may show

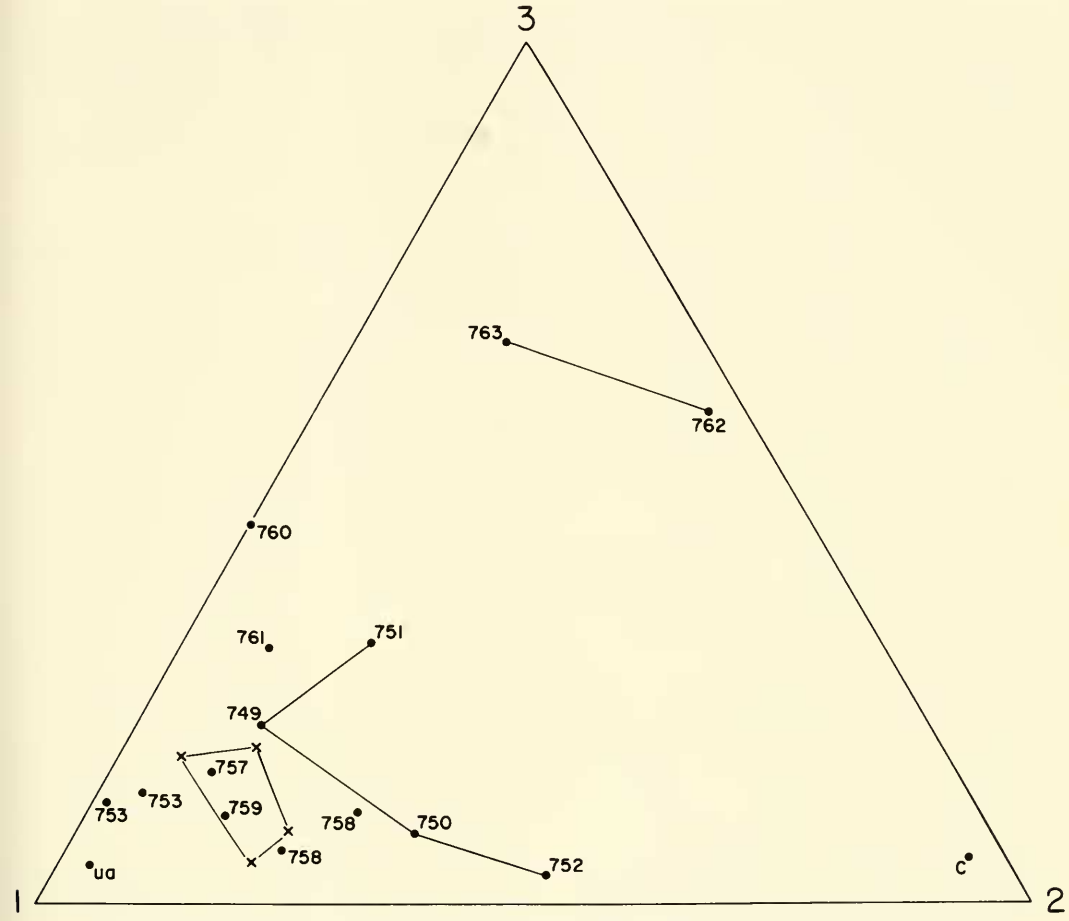


Figure 16. Loadings for South Caicos samples on first three varimax axes. Symbols as on Figure 14.

slightly elevated levels of genetic variability (P, H) and are frequently characterized by the segregation of rare or unique alleles at frequencies far higher than those seen in homospecific populations (Woodruff, 1981). In addition, several step clines in allele frequencies are associated with the hybrid zone. The pattern of clinal variation (bank-edge to bank-interior coasts) of several alleles on New Providence ($6Pgd^{1.0}$, $Es\text{-}2^{1.09}$, $Pgm\text{-}2^{1.2}$) is, in fact, quite similar to that seen on South Caicos and Providenciales. The obvious question arising from the similarities of New Providence and South Caicos is whether today's South Caicos populations represent the legacy of a historical interaction between two species? Has the evidence for a former bank-interior species all but disappeared on this smaller island?

If the Caicos Bank had been originally occupied by a bank-edge and a bank-interior species comparable to those seen on the Great Bahama Bank and the Little Bahama Bank islands, we would make two predictions about the situation on South Caicos based on our earlier work. First, the island is too small for genetically "pure" populations of the interior taxon to endure. All living populations are found within 7 km of the bank-edge and will therefore be introgressed to varying degrees. Present

island size limits our ability to examine this prediction. Nevertheless, additional collecting on bank-interior coasts of North Caicos, Grand Caicos and East Caicos might illuminate this issue as such populations live >10 km from the modern bank-edge coasts. Second, we would predict that the populations furthest from the bank-edge coasts will show more evidence for hybridity than those at the coast. Such interior populations as 764 and 762 might show elevated levels of *P* or *H*, increased heterozygote deficiency or excess, or higher frequencies of rare or unique alleles. There is, however, no evidence for consistent geographic trends in *P*, *H*, or departure from random mating. Only in the case of the rare allele phenomenon are the interior populations at all unusual. Unexpected alleles were, in fact, detected in samples 764 and 762 at Aat^{07}, $Es\text{-}2^{11}$, $Es\text{-}2^{12}$, and $6Pgd^{08}$ at frequencies of 0.02–0.05. Additional rare alleles occurred at 759–761, sites which are also geographically intermediate between the bank-edge and the bank-interior coasts: $Pgm\text{-}2^{13}$, $Mdh\text{-}1^{12}$, Aat^{04}. Two of these rare alleles ($6Pgd^{08}$ and $Es\text{-}2^{11}$) were also detected on Providenciales in sample 772 from the southern bank-interior coast. These rare alleles may be a legacy of a former hybrid zone—that is, they may constitute the genetic anomaly seen in other *Cerion* hybrid zones. Alternatively, these currently rare alleles may once have occurred at higher frequencies in the conspecific bank-interior populations of *C. regina* that until a few thousand years ago occupied an area 20 times as extensive as today's islands.

These hints of genetic vestiges for another taxon within *C. regina* are intriguing (see final section), but do not alter our conclusion that all indigenous *Cerion* so far collected in the Turks and Caicos (excluding the recent immigrants *C. blandi* and *C. lewisi*) belong to the single species *C. regina*. Interspecific hybridization is so rampant in *Cerion* (Woodruff and Gould, 1987) that most widespread species of *Cerion* probably maintain, at least in parts of their range, introgressed genetic material of other taxa. When these introgressed contributions are minor and, especially (as here) when they are associated with no morphological expression of intermediacy, we must retain the name of the dominant component.

We faced the same problem in determining the proper name of the mottled morphotype on New Providence Island (Gould and Woodruff, 1986). *C. gubernatorium*, the oldest name, was originally given to populations that contain "phantom" genes of *C. agassizi*, a prominent fossil taxon now extinct on New Providence, but still living on the adjacent islands of Cat and Eleuthera (and also hybridizing with mottled *Cerion* in both places). Despite these genetic "phantoms," and some morphological remnant of *C. agassizi* as well, we accepted *C. gubernatorium* as the correct name for all mottled *Cerion* of New Providence because the *C. agassizi* signature in these populations is so small relative to the morphological and genetic expression of ordinary (and abundant) mottled *Cerion*. The evidence for phantoms of another taxon within some samples of *C. regina* is far weaker, and shall not alter our taxonomic conclusion that all known Turks and Caicos samples of the tapering morphotype belong to the single species, *C. regina*. We must, however, bear in mind what is no longer only the intriguing possibility, but by now the established fact that important features of geographic variability within many *Cerion* taxa are the product of introgression, not simple local adaptation.

VIII. Level Four: Covariation Within Samples

Variation in average form among samples (treated in all previous sections), and differences among organisms within a population, are so fundamentally distinct in concept that we anticipate no necessary relationship between their patterns. Yet all *Cerion* species grow with the same allometries (despite enormous differences in

TABLE 11. SCORES FOR FIVE-AXIS SOLUTION OF SPECIMENS WITHIN SAMPLE 753.

Measure	Axis 1	Axis 2	Axis 3	Axis 4	Axis 5
1. PROWID	0.242	0.020	0.240	0.125	−0.130
2. FOURWID	0.387	0.166	0.075	0.094	−0.025
3. NUMWHO	−0.216	−0.402	0.133	0.027	0.024
4. RIBDENS	−0.064	−0.084	0.358	0.206	0.071
5. LENGTH	0.065	−0.314	0.075	−0.158	0.054
6. WIDTH	0.308	−0.109	−0.009	−0.220	0.180
7. PROHT	−0.117	−0.052	0.539	−0.144	0.204
8. FOURHT	0.205	0.168	0.408	0.106	−0.116
9. FRSXHT	0.365	0.178	0.179	0.113	−0.051
10. UMBWID	0.013	0.126	0.320	0.184	0.367
11. LIPWID	0.258	−0.089	−0.061	0.101	0.143
12. LIPTHK	0.019	−0.239	0.029	0.185	−0.045
13. APHT	0.287	−0.094	−0.085	−0.233	0.443
14. APWID	0.254	−0.147	−0.181	−0.033	0.317
15. APROT	−0.065	−0.041	−0.058	0.476	0.294
16. EC	0.075	−0.407	−0.088	0.245	−0.245
17. FA	0.259	−0.295	0.194	−0.205	−0.352
18. APTILT	−0.131	−0.024	−0.030	0.435	0.191
19. WEIGHT	0.049	−0.292	0.092	−0.129	0.175
20. HWRATIO	−0.140	−0.344	0.190	0.063	−0.079
21. PRORAT	0.304	−0.042	−0.119	0.342	−0.264
22. FOURRAT	0.175	−0.243	−0.203	0.158	0.130

outcome), and the gastropod shell, in general, is a highly constrained structure replete with geometrically forced covariances. Thus, we expect that similar patterns might regulate the different styles of within- and among-sample variation (see Gould and Paull, 1977; Gould and Woodruff, 1978 for correspondences in other *Cerion* species). Sample means might represent different states along tracks of covariance common to the within-sample variation of all populations.

Since all shells are adults and their range in size is not large, our samples of 20 do not provide enough specimens for stable covariance structures within populations (though they define mean values adequately). But we measured a larger number of shells (as a split sample to test for proximity in morphospace) for South Caicos *C. regina* at locality 753 (35 individuals). Table 11 presents factor scores for this enlarged sample. The structure of covariation is stable at five meaningful axes (93.2% of information). (In a sequence of reduction from 10 axes down, none of the first five axes ever dip below 7%, and no subsequent axis reaches 2% of total information.)

The first axis unites the two major patterns of constrained covariance that we have discussed throughout this paper. First, we see all chief components of the compensatory (flat top with later height) covariance that sets the primary pathway of variation in shape from obtusely triangular in cross section throughout, to distinctly flat topped at first, and parallel-sided during later growth. Note high scores for the two ratio measures of flat top (width/height of protoconch at 0.304, and of the fourth whorl at 0.175). Protoconch width (0.242) greatly exceeds protoconch height (negative at −0.117), but height is beginning to catch up by the fourth whorl (0.387 for width, 0.205 for height). The three scores for successive heights increase continually to record the compensation (−0.117 to 0.205 to 0.365).

Second, we note all elements of the major constraint imposed by geometric necessity: large whorls imply fewer adult

whorls under conditions of restricted range in adult size. Intermediate standardized whorl sizes score highly (fourth width and height at 0.387 and 0.205, and fourth to sixth height at 0.365). These large whorls imply fewer total whorls (−0.216), with the usual consequence of squatter adult shells, since later whorls add relatively more height than width (height/width ratio of adult shell at −0.140).

The second axis primarily records whorl number (−0.402) and its consequences in shape for a high, but not wide, shell (−0.314 for height, −0.109 for width, since later whorls add relatively more height than width), and final shape (height/width ratio at −0.344). This primary association also brings along, as on axis 1, the forced negative covariances with standardized whorl sizes (0.166 for fourth width, 0.168 for fourth height, 0.178 for fourth to sixth height).

The highest scores on the third axis are for early standardized heights (0.539 for the protoconch, 0.408 for the fourth whorl), with protoconch width also scoring at 0.240. We do not understand the basis for associated high scores of umbilicus (0.320) and density of ribbing (0.358).

The smaller fourth and fifth axes express different aspects of the third allometric phase that builds *Cerion*'s aperture. The fourth axis records its two highest scores for measures of intensity in the change of orientation made by the growing edge before it deposits the definitive adult aperture (0.476 for apertural rotation, 0.435 for tilt). The fifth axis records the size of the expanded apertural mouth (0.443 and 0.317 for apertural height and width, associated with negative values for the penultimate whorl heights overgrown by this expansion, −0.245 and −0.352 for measures 16 and 17).

In summary, each axis makes sense in terms of both the general geometry of shell coiling (the whorl size versus whorl number principle for example), and the peculiarities of *Cerion*'s own universal pattern of growth (the apertural changes at adulthood, and the allometric compensation of flat top by later height, for example). We find interesting similarities and differences with patterns of covariation at the between-sample levels considered earlier. Dominating the within-sample system, we find two covariance sets that also regulate variation among mean vectors of *C. regina* samples—the compensatory shape covariance (setting axis one here), and the negative interaction of whorl size and number (expressed on both first and second axes). Most different from between-sample patterns are the greater strength of these two covariance sets, and absence of the general size factor that played an important role at all higher levels. Interestingly, these two differences are causally related. The size factor is absent here for the simple reason that size varies little among adults within most populations (length ranges from 27.0 to 34.0 mm in this sample), but greatly in mean values among populations (see appendix). The constraint covariance (whorl size versus whorl number) only operates when size ranges are small and restricted (see Gould and Paull, 1977 for quantitative demonstration)—for if adult size is free to vary, then large early whorls need not be compensated by growing fewer whorls to reach a limited final size.

To assess the generality of these within-sample covariances across taxa, we present, as Table 12, factor scores for the four large and interpretable axes (90.9% of information) of a *C. lewisi* sample (No. 221564, see appendix). The axes are remarkably similar to those noted just above in *C. regina*. High scores on the first axis emphasize *C. lewisi*'s chief character of many whorls and its consequence for slender shape (0.484 for whorl number, 0.323 for adult height, with adult width much less at 0.170, and 0.281 for height/width ratio of the adult shell). But we also note the constraint covariance, operating on this axis in the negative scores for standardized whorl sizes (−0.104 and −0.099 for protoconch and fourth width; −0.203 and

TABLE 12. SCORES FOR FOUR-AXIS SOLUTION OF SPECIMENS WITHIN A SAMPLE OF *C. LEWISI*.

	Measure	Axis 1	Axis 2	Axis 3	Axis 4
1.	PROWID	−0.104	0.362	−0.241	0.032
2.	FOURWID	−0.099	0.130	−0.185	0.171
3.	NUMWHO	0.484	−0.095	0.003	−0.024
4.	RIBDENS	0.344	0.284	0.434	0.133
5.	LENGTH	0.323	−0.050	−0.072	0.209
6.	WIDTH	0.170	−0.035	−0.209	0.140
7.	PROHT	0.048	0.330	0.210	0.140
8.	FOURHT	−0.203	0.454	−0.013	0.279
9.	FRSXHT	−0.178	0.315	−0.188	0.098
10.	UMBWID	0.036	0.309	0.143	0.014
11.	LIPWID	0.147	0.196	−0.324	−0.155
12.	LIPTHK	0.193	0.167	−0.042	−0.181
13.	APHT	0.123	−0.099	−0.240	0.306
14.	APWID	0.080	−0.155	−0.290	0.166
15.	APROT	−0.050	−0.109	−0.100	0.468
16.	EC	0.125	0.010	0.004	0.359
17.	FA	0.258	0.327	−0.119	−0.182
18.	APTILT	0.054	−0.092	0.023	0.430
19.	WEIGHT	0.208	0.036	−0.094	0.008
20.	HWRATIO	0.281	0.081	0.139	0.063
21.	PRORAT	−0.054	0.114	−0.437	−0.100
22.	FOURRAT	0.352	−0.011	−0.278	−0.153

−0.178 for fourth, and fourth to sixth whorl height).

The second axis, as did the third in *C. regina*, emphasizes standardized whorl sizes and little else. We are again puzzled that both ribbing (at 0.284) and umbilical width (at 0.309) also score strongly, for they did in *C. regina* as well, and we do not understand the basis for such an association—though its discovery in two taxa suggests a possible generality.

The third axis expresses the compensatory shape covariance that so dominates geographic sorting (both within and between islands) of *C. regina*, and also the first axis of within-sample covariation in *C. regina* sample 753. Its existence in *C. lewisi* supports our claim that this association is an important principle governing *Cerion*'s shape throughout the genus. The shell begins flat, with high score for protoconch width (−0.241) and opposite score for protoconch height (0.210—the factor loadings of all specimens are negative on this axis, so we discuss negative scores as high values). This initial flatness is recorded in high scores for width/height ratios of protoconch (−0.437) and fourth whorl (−0.278). But later heights compensate, and we note the continual gradient in scores for the three standardized heights that we have observed so many times before (+0.210, −0.013 and −0.188 for protoconch, fourth, and fourth to sixth whorls).

The fourth axis amalgamates the two apertural covariance sets that formed the fourth and fifth axes of *C. regina*. We note high scores for the two measures of change in orientation (0.468 for rotation, 0.430 for tilt) and for apertural size (0.306 for height, 0.166 for width).

The patterns of within-sample covariance for representative samples of two species are therefore similar to each other, and different from between-sample patterns in the same ways. In both, we find no general size axis since the within-sample range of shell size is small. In both, the compensatory shape covariance (flat top and later height) and the constraint covariance (whorl size versus whorl number) dominate the larger axes. The constraint

covariance appears more strongly in these within-sample patterns because it only operates when the range of final size is limited. In both samples, we also find sensible associations for measures of the aperture and standardized whorl sizes. We believe that we are here looking through a glass not so darkly at the general rules of growth within *Cerion*.

IX. Conclusion and Prospect

This work begins the second half of our long-term project to revise the Bahamian *Cerion* in the light of new data and contemporary concepts of evolution. It is our initial study, following our strategy of beginning with geographic outliers that maintain low diversity, of *Cerion* faunas in the southeastern Bahamas—a group of species different from those of Great and Little Bahama banks, the subjects of our previous work. We will move from here to the complexity of the largest island, Great Inagua, where more taxa (about 20) have been designated, and at least three widespread indigenous species actually exist.

A close relative of *C. regina* inhabits the long bank-edge northern coast of Great Inagua. But Inagua is big and diverse enough to maintain other indigenous *Cerion* species—including the vast populations of the island interior and bank-interior coasts (now called *C. rubicundum* and *C. dalli*, but probably belonging to a single species), and the widespread dwarfed *C.* (*Umbonis*) that lives in true sympatry (the first unambiguously recorded case in the entire genus *Cerion*) with both bank-edge and interior species. The small islands that we studied in the Turks and Caicos maintain only the bank-edge species as a widespread, indigenous form—but they permit us, by extension, to grasp the greater complexity of Inagua.

It is often said of historical sciences like ours (said, that is, by those who would degrade our activity, or bar us completely from the realm of science) that we traffic only in the narrative description of particulars and that we never predict or derive any generalities worthy of the name. Narrative must be treasured in its own right (for it can be every bit as factual as anything in science), but science must aspire to more—as historical science does, despite the caricatured dismissal outlined above.

The complexities and contingencies of history do preclude detailed prediction of future events, but prediction of this sort does not lie within our domain. Yet historical scientists work with a sort of prediction all the time—of events that have happened but have not yet been revealed by evidence, or of current situations inferred but not yet validated. In this essential component of generalization, natural historians work like all scientists.

Yet many of our subjects are so resolutely particular that we cannot proceed beyond simple narrative; thus, we must seek and exploit those situations of sufficient repetition to permit the apprehension of general pattern within the particulars. The attraction of *Cerion* lies in its central source of both narrative and generality—its overwhelming diversity, repeated in all ways that we can study: morphologically, genetically, biogeographically, ecologically.

Thus, we feel that we can creep to the end of an inferential limb and predict (based on genetic hints) that a second indigenous, geographically interior taxon may still persist (either as relatively pure populations or as substantial introgressed contributions to *C. regina*) in the centers of large islands on the Caicos Bank. We say this for two reasons: first, we have traced central distinctions between bank-edge and interior taxa on many other islands; second, we can often document the disappearance of the interior taxon on small islands that are, so to speak, "all" bank-edge, while the interior taxon persists on adjacent larger islands (for example, both bank-edge and interior *Cerion* live on Great Exuma, but only the bank-edge species on all the small adjacent cays). We also predict (based on repeated pattern from nearby Great Inagua), that should

this interior taxon be found, it will bear a smaller, thinner and more mottled shell than typical *C. regina* (we base this inference on the bank-edge versus interior distinction on all other islands, and particularly on the Inaguan separation between interior *C. rubicundum* and *C. columna*, the bank-edge analog of *C. regina*).

Likewise, our studies of allometry and ontogenetic covariance provide a basis for ordering variation within species (and often between hybridizing taxa) in a sensible way. The patterns dictated by what we have called the constraint and compensatory covariances are sensibly interpreted as necessary outcomes of *Cerion*'s basic ontogeny; they then determine the correlated consequences of any primary change in size or shape. And they occur over and over again in predictable manners and circumstances.

We find it intellectually satisfying that the primary component of narrative—*Cerion*'s buzzing and blooming outpouring of diversity—also becomes raw material for the repetitions that science requires for discussing general pattern. As great naturalists (G. E. Hutchinson, for example) exemplify by their life and work, exultation and explanation are complementary aspects of nature and its impact upon our minds.

LITERATURE CITED

AVISE, J. C., AND C. F. AQUADRO. 1982. A comparative summary of genetic distances in the vertebrates. Patterns and correlations. Evolutionary Biology, **15:** 151–185.

AYALA, F. J. 1983. Enzymes as taxonomic characters, pp. 3–26. *In* G. S. Oxford and D. Rollinson (eds.), Protein Polymorphism: Adaptive and Taxonomic Significance. New York, Academic Press.

CAIN, A. J., AND J. P. CURREY. 1963. Area effects in *Cepaea*. Heredity, **18:** 467–471.

CLENCH, W. J. 1937. Descriptions of new land and marine shells from the Bahama Islands. Proceedings of the New England Zoological Club, **16:** 17–26.

———. 1957. A catalogue of the Cerionidae (Mollusca-Pulmonata). Bulletin of the Museum of Comparative Zoology, **116:** 121–169.

———. 1961. Land and freshwater mollusks of Caicos, Turks, Ragged islands and the islands on the Cay Sal Bank, Bahamas. Occasional Papers on Mollusks, Museum of Comparative Zoology, Harvard Univ., **2**(26): 229–259.

CLENCH, W. J., AND C. G. AGUAYO. 1952. The *scalarinum* species complex (*Umbonis*) in the genus *Cerion*. Occasional Papers on Mollusks, Museum of Comparative Zoology, Harvard Univ., **1:** 413–440.

CRAMPTON, H. E. 1916. Studies on the variation, distribution, and evolution of the genus *Partula*. The species inhabiting Tahiti. Carnegie Institute of Washington Publication, **228:** 1–311.

———. 1925. Studies on the variation, distribution, and evolution of *Partula*. The species of the Mariana Islands, Guam and Saipan. Carnegie Institute of Washington Publication, **228A:** 1–116.

———. 1932. Studies on the variation, distribution, and evolution of *Partula*. The species inhabiting Moorea. Carnegie Institute of Washington Publication, **410:** 1–335.

DEVRIES, W. 1974. Caribbean land molluscs: notes on Cerionidae. Studies Fauna Curaçao and other Caribbean Islands, **45:** 81–117.

GALLER, L., AND S. J. GOULD. 1979. The morphology of a "hybrid zone" in *Cerion*: variation, clines, and an ontogenetic relationship between two "species" in Cuba. Evolution, **33**(2): 714–727.

GOULD, S. J. 1969a. Character variation in two land snails from the Dutch Leeward Islands: geography, environment, and evolution. Systematic Zoology, **18:** 185–200.

———. 1969b. An evolutionary microcosm: Pleistocene and recent history of the land snail *P.* (*Poecilozonites*) in Bermuda. Bulletin of the Museum of Comparative Zoology, **138:** 407–532.

———. 1984a. Covariance sets and ordered geographic variation in *Cerion* from Aruba, Bonaire and Curaçao: a way of studying nonadaptation. Systematic Zoology, **33**(2): 217–237.

———. 1984b. Morphological channeling by structural constraint: convergence in styles of dwarfing and gigantism in *Cerion*, with a description of two new fossil species and a report on the discovery of the largest *Cerion*. Paleobiology, **10**(2): 172–194.

GOULD, S. J., AND C. PAULL. 1977. Natural history of *Cerion*. VII. Geographic variation in *Cerion* (Mollusca: Pulmonata) from the eastern end of its range (Hispaniola to the Virgin Islands): coherent patterns and taxonomic simplification. Breviora, **445:** 1–24.

GOULD, S. J., AND D. S. WOODRUFF. 1978. Natural history of *Cerion*. VIII. Little Bahama Bank—a revision based on genetics, morphometrics, and geographic distribution. Bulletin of the Museum of Comparative Zoology, **148**(8): 371–415.

———. 1986. Evolution and systematics of *Cerion* (Mollusca: Pulmonata) on New Providence Is-

land: a radical revision. Bulletin of the American Museum of Natural History, **182**(4): 389–490.

Gould, S. J., N. D. Young, and B. Kasson. 1985. The consequences of being different: sinistral coiling in *Cerion*. Evolution, **39:** 1364–1379.

Gulick, J. T. 1905. Evolution racial and habitudinal. Carnegie Institute of Washington Publication, **25:** 1–269.

Hummelinck, P. W. 1940. Mollusks of the genera *Cerion* and *Tudora*. Studies Fauna Curaçao, Aruba, Bonaire and the Venezuelan Islands No. 5.

Jolicoeur, P. 1963. The multivariate generalization of the allometry equation. Biometrics, **19:** 497–499.

———. 1984. Principal components, factor analysis, and multivariate allometry: a small-sample direction test. Biometrics, **40:** 685–690.

Maynard, C. J. 1889. Monograph of the genus *Strophia*. *In* Contributions to Science, vol. 1. Newtonville, Mass., self-published.

Maynard, C. J., and N. A. Clapp. 1919–26. Contributions to the history of the Cerionidae, with descriptions of many new species and notes on evolution in birds and plants. Appendix to vol. 10. Records of walks and talks with nature. West Newton, Mass., self-published, 242 pp.

Murray, J., and B. Clarke. 1980. The genus *Partula* on Moorea: speciation in progress. Proceedings of the Royal Society of London, **211:** 83–117.

Nei, M. 1978. Estimation of average heterozygosity and genetic distance from a small number of individuals. Genetics, **89:** 583–590.

Pilsbry, H. A., and E. G. Vanatta. 1895. New species of the genus *Cerion*. Proceedings of the Academy of Natural Sciences of Philadelphia, pp. 206–210.

———. 1896. Catalogue of the species of *Cerion*, with descriptions of new forms. Proceedings of the Academy of Natural Sciences of Philadelphia, pp. 315–338.

Raup, D. M. 1966. Geometric analysis of shell coiling: general problems. Journal of Paleontology, **40:** 1178–1190.

Selander, R. K., and T. S. Whittam. 1983. Protein polymorphism and the genetic structure of populations. *In* M. Nei and R. K. Koehn (eds.), Evolution of Genes and Proteins. Sunderland, Mass., Sinauer Assoc.

Swofford, D. L., and R. B. Selander. 1981. BIOSYS-1. A Computer Program for the Analysis of Allelic Variation in Genetics. Users manual. Urbana, Univ. of Illinois, 65 pp.

Woodruff, D. S. 1975. Allozyme variation and genic heterozygosity in the Bahamian pulmonate snail *Cerion bendalli*. Malacological Review, **8:** 47–55.

———. 1981. Towards a genodynamics of hybrid zones. *In* W. D. Atchley and D. S. Woodruff (eds.), Essays on Speciation and Evolution in Honor of M. J. D. White. Cambridge, Cambridge Univ. Press.

Woodruff, D. S., and S. J. Gould. 1980. Geographic differentiation and speciation in *Cerion*: a preliminary discussion of patterns and processes. Biological Journal of the Linnean Society, London, **14:** 389–416.

———. 1987. Fifty years of interspecific hybridization: genetics and morphometrics of a controlled experiment involving the land snail *Cerion* in the Florida Keys. Evolution.

Wright, S. 1978. Evolution and the Genetics of Populations, vol. 4, Variability within and among Natural Populations. Chicago, Univ. of Chicago Press.

APPENDIX: MATRIX OF MEANS FOR ALL SAMPLES.*

No.	Sample name	1 PROWID	2 FOURWID	3 NUMWHO	4 RIBDENS	5 LENGTH	6 WIDTH	7 PROHT	8 FOURHT	9 FRSXHT
1.	758T SC	53.00	74.00	7.806	12.75	30.85	12.00	21.25	58.30	70.40
2.	753A SC	53.00	75.50	7.898	13.88	30.81	12.29	21.69	57.06	67.94
3.	116022 SC	48.90	66.19	7.185	11.19	24.45	9.70	19.86	56.00	62.92
4.	189858 NC	57.50	72.05	7.506	12.63	27.17	10.36	25.90	65.65	63.50
5.	189859 MC	55.43	70.29	7.813	11.43	29.15	11.09	24.64	59.21	62.62
6.	219190 LC	52.80	76.35	7.588	13.30	29.21	12.04	21.50	57.45	71.37
7.	219192 GC	51.65	65.65	8.113	13.80	29.37	10.70	23.80	55.55	57.40
8.	219194 EC	55.00	74.00	7.698	12.71	31.33	11.90	24.50	58.08	71.75
9.	219195 GC	55.00	69.15	7.813	13.25	29.56	11.07	25.40	59.70	64.00
10.	219196 GC	52.70	68.85	7.400	14.40	27.02	10.51	21.95	60.20	63.85
11.	219197 EC	52.00	68.00	8.625	13.61	32.29	11.70	24.65	55.88	57.56
12.	219199 EC	53.06	71.19	7.477	15.50	27.31	10.69	20.94	57.88	65.88
13.	219200 EC	53.20	66.80	8.100	16.90	28.88	11.06	24.95	55.95	56.60
14.	219201 NC	51.20	61.05	8.544	17.65	29.25	9.96	26.15	55.05	49.90
15.	220898 LC	53.75	72.85	7.144	12.87	24.70	11.01	26.50	60.45	62.78
16.	220899 SAND	45.80	63.40	6.581	16.55	19.24	8.80	22.05	56.80	56.84
17.	220905 B	49.95	64.45	8.081	12.55	28.54	11.08	27.15	59.25	56.80
18.	220906 B	50.15	65.50	8.119	15.55	29.38	11.50	27.55	59.10	57.35
19.	220907 B	48.25	60.30	7.956	16.80	27.54	10.09	26.05	57.80	56.10
20.	220908 B	46.80	59.05	7.681	14.60	24.53	9.27	25.60	57.30	55.90
21.	220909 B	48.10	61.80	8.044	14.00	27.81	10.34	26.20	56.65	56.30
22.	220910 B	48.05	62.45	8.044	15.00	28.46	10.34	25.00	57.55	57.84
23.	220911 B	45.55	59.65	7.769	12.20	24.37	9.69	26.70	55.35	53.15
24.	220912 B	51.45	66.15	7.419	13.50	25.94	10.55	26.15	62.40	61.31
25.	220913 B	52.15	68.80	7.738	12.80	27.50	11.20	27.20	62.15	61.60
26.	220914 B	50.95	70.55	7.431	15.15	27.15	11.40	25.35	60.60	65.88
27.	221564 LPC	52.35	60.95	8.188	13.80	29.07	9.69	25.45	56.90	53.90
28.	221565 LFGC	49.70	56.60	8.031	15.65	25.36	8.70	25.25	54.55	48.89
29.	221566 LPARC	50.70	59.20	8.744	15.75	29.59	9.84	24.45	52.05	46.20
30.	221567 LWATC	55.60	64.55	7.831	12.50	28.21	9.94	26.00	58.95	59.16
31.	221568 LWC	49.78	60.11	7.306	15.22	22.21	8.79	25.78	56.11	50.40
32.	221569 LPR	48.08	57.20	7.790	13.88	25.36	8.54	23.84	55.08	53.45
33.	221570 LPR	53.40	62.00	8.138	14.40	27.12	9.32	25.30	56.80	52.60
34.	749 SC	51.20	69.45	7.756	11.72	28.38	11.22	22.00	54.65	63.05
35.	750 SC	52.00	69.60	7.500	11.29	27.44	10.57	21.35	57.05	66.24
36.	751 SC	50.70	68.60	7.588	10.00	27.16	10.71	20.85	53.10	64.20
37.	752 SC	52.10	71.15	7.300	11.26	26.05	10.67	20.45	56.20	64.54
38.	753 SC	54.10	77.40	7.888	11.25	32.09	12.84	20.55	55.85	68.15
39.	REG	56.95	70.15	7.094	12.30	25.79	9.98	25.40	65.35	62.17
40.	757 SC	52.63	74.16	7.803	13.21	30.71	12.18	20.32	55.16	69.53
41.	758 SC	53.15	73.95	7.906	12.15	30.94	11.91	21.30	58.15	67.50
42.	759 SC	53.25	72.85	7.756	11.16	30.11	11.83	21.15	56.90	67.75
43.	760 SC	50.20	69.05	7.881	13.11	28.52	11.38	19.75	52.65	62.50
44.	761 SC	50.05	70.55	7.731	15.05	28.10	10.93	20.55	55.05	64.30
45.	762 SC	48.95	64.40	7.400	10.90	24.94	9.67	20.00	53.75	62.29
46.	763 SC	49.33	64.53	7.683	15.13	26.55	10.15	20.67	52.80	62.47
47.	766 GT	53.33	76.11	7.944	10.11	32.08	12.41	24.44	63.11	67.00
48.	769 GT	51.30	77.20	7.688	14.10	29.67	11.70	24.30	62.00	69.75
49.	770 PR	58.00	73.25	7.619	15.10	28.83	11.08	26.80	63.95	64.75
50.	771 PR	59.40	71.90	7.519	16.30	28.40	10.63	27.90	66.20	64.83
51.	772 PR	51.70	65.40	7.575	15.21	26.14	10.16	23.80	57.45	61.63
52.	780 GT	52.25	75.10	7.419	13.05	28.14	11.31	24.50	64.75	68.36
53.	781 GT	52.35	70.90	8.244	13.80	31.38	11.80	25.25	59.70	63.20
54.	782 GT	54.75	73.15	8.094	13.30	30.32	11.97	27.00	62.90	61.25
55.	783 GT	55.15	75.75	8.125	13.45	32.64	12.41	25.20	63.00	66.15
56.	SCFOSIS	55.35	75.65	8.360		36.05	13.25	22.71	58.00	67.53

APPENDIX: CONTINUED.

10 UMBWID	11 LIPWID	12 LIPTHK	13 APHT	14 APWID	15 APROT	16 EC	17 FA	18 APTILT	19 WEIGHT	20 HW RATIO	21 PRORAT	22 FOUR-RAT
32.50	19.7	26.0	100.90	78.90	26.63	52.11	25.00	2.11	1.62	2.57	2.53	1.28
34.69	26.1	34.6	107.33	88.50	30.75	51.31	19.88	2.79	1.40	2.51	2.46	1.33
24.62	19.1	19.7	81.33	66.24	20.43	42.19	22.57	1.90	0.63	2.52	2.47	1.19
24.00	20.5	21.5	86.50	71.45	22.45	41.35	18.70	2.32	0.64	2.62	2.23	1.10
27.93	20.9	29.7	92.21	74.29	20.79	46.93	25.07	1.91	0.92	2.63	2.25	1.19
32.45	20.7	27.5	100.70	84.30	29.80	53.80	20.40	2.71	1.59	2.43	2.47	1.33
25.30	22.5	26.3	93.60	74.65	25.25	45.85	22.00	2.17	1.00	2.75	2.19	1.18
26.82	26.6	37.6	104.27	83.45	27.73	59.27	28.45	2.08	1.89	2.64	2.26	1.28
26.55	25.5	36.7	94.45	77.30	24.10	49.80	25.00	2.05	1.33	2.67	2.18	1.16
25.35	23.4	28.7	88.20	74.85	23.00	45.60	23.20	2.01	0.66	2.57	2.42	1.14
35.39	25.2	30.1	101.72	83.94	31.50	47.39	17.17	3.04	1.08	2.75	2.12	1.22
26.88	25.1	26.1	91.25	74.19	24.75	44.44	22.88	1.98	1.00	2.55	2.55	1.23
28.80	23.0	25.9	94.05	76.40	25.75	47.65	21.50	2.26	0.89	2.61	2.14	1.20
22.50	20.3	25.4	87.20	70.60	25.45	51.00	23.10	2.31	0.90	2.94	1.96	1.11
26.60	18.0	31.1	81.15	69.50	19.55	48.75	24.25	2.04	1.36	2.25	2.04	1.21
23.00	13.8	18.1	69.50	58.67	20.38	33.40	11.06	3.18	1.19	2.20	2.08	1.12
34.30	22.1	22.2	89.60	71.15	28.10	45.05	21.00	2.27	0.59	2.58	1.84	1.09
34.60	20.1	21.3	92.25	68.00	25.85	45.00	22.45	2.07	1.32	2.56	1.83	1.11
28.65	20.3	16.0	85.95	65.85	25.85	43.75	21.05	2.14	0.85	2.74	1.86	1.04
26.80	17.2	14.9	78.05	60.85	24.05	39.50	19.35	2.06	0.58	2.65	1.83	1.03
29.95	20.1	18.0	87.85	65.15	28.40	41.70	20.40	2.10	0.74	2.69	1.84	1.09
29.30	21.4	18.2	88.35	66.65	26.75	44.50	21.65	2.15	0.78	2.75	1.94	1.09
27.55	16.6	16.4	74.50	56.20	23.65	37.00	20.90	1.83	0.81	2.52	1.72	1.08
30.05	22.4	24.1	83.35	68.25	21.85	43.75	23.95	1.85	1.11	2.46	1.97	1.06
34.00	20.5	19.8	84.85	66.75	22.90	40.30	23.50	1.75	1.42	2.46	1.93	1.11
33.60	20.8	20.2	88.85	74.25	24.45	46.55	25.35	1.87	1.19	2.39	2.02	1.17
20.75	18.6	24.8	86.85	67.70	21.85	49.05	26.10	1.89	0.83	3.00	2.06	1.07
21.35	16.9	17.1	76.90	61.70	22.85	42.45	19.80	2.28	0.60	2.92	1.98	1.04
21.70	19.7	24.7	88.20	68.45	23.60	44.60	20.55	2.23	0.91	3.01	2.08	1.14
20.85	19.0	22.1	87.25	69.65	23.80	47.65	24.95	1.96	0.86	2.84	2.15	1.10
20.60	15.4	17.6	69.89	58.22	19.00	37.44	19.00	2.03	0.72	2.53	1.93	1.07
17.40	15.7	17.8	77.80	60.68	22.56	43.52	20.60	2.16	0.54	2.96	2.03	1.04
18.90	16.6	19.0	78.80	60.70	20.30	42.10	23.30	1.82	0.84	2.91	2.12	1.10
24.15	21.5	35.4	93.00	78.60	25.80	52.35	25.50	2.10	1.28	2.54	2.33	1.27
23.40	22.9	28.5	90.60	74.40	25.70	46.80	22.65	2.11	1.16	2.60	2.45	1.22
25.50	18.8	22.1	89.15	73.35	23.70	50.75	24.70	2.08	1.05	2.54	2.45	1.30
25.80	19.9	25.9	86.25	72.40	20.85	48.25	25.00	1.98	1.08	2.44	2.56	1.27
35.20	30.1	40.4	110.95	93.65	31.55	53.85	22.50	2.49	1.47	2.50	2.65	1.39
22.85	19.1	23.8	83.40	67.60	22.75	44.10	22.40	2.00	0.98	2.58	2.26	1.08
32.32	23.3	28.4	103.89	86.63	28.79	56.74	25.74	2.39	1.22	2.52	2.60	1.35
30.35	21.2	27.1	99.53	82.65	28.30	55.40	28.25	2.02	1.32	2.60	2.53	1.27
33.20	25.0	31.1	100.80	83.65	30.00	49.65	23.85	2.17	1.21	2.55	2.55	1.28
35.00	22.9	39.6	96.55	82.50	29.10	48.05	18.70	2.75	1.03	2.51	2.55	1.31
30.15	20.1	31.1	92.45	76.80	29.00	48.95	22.75	2.23	1.13	2.58	2.46	1.28
24.75	20.1	16.9	82.00	65.60	22.40	42.90	21.25	2.07	0.44	2.58	2.46	1.20
26.40	18.4	23.5	85.93	70.79	22.43	51.40	24.00	2.17	1.02	2.61	2.40	1.22
30.89	21.0	19.7	102.00	80.33	27.11	52.33	26.33	2.02	1.28	2.58	2.19	1.21
31.90	24.6	12.0	99.40	79.55	29.50	50.55	23.10	2.26	0.92	2.54	2.12	1.25
27.80	20.6	21.4	95.25	76.45	27.95	51.80	22.85	2.33	0.95	2.61	2.18	1.15
27.95	23.1	26.2	92.90	75.10	25.05	48.55	23.90	2.07	1.13	2.67	2.14	1.09
27.90	17.3	18.3	84.55	71.20	24.95	45.95	24.90	1.91	0.66	2.57	2.18	1.14
32.35	19.9	17.7	91.05	72.75	27.25	47.90	23.65	2.08	0.85	2.49	2.15	1.16
34.60	22.7	22.9	100.45	80.05	32.45	49.60	20.00	2.66	1.21	2.66	2.08	1.19
35.05	20.4	19.9	94.60	77.95	29.55	52.35	24.10	2.23	1.13	2.53	2.04	1.16
35.60	24.8	22.5	105.10	82.00	31.85	53.80	23.25	2.39	1.22	2.63	2.19	1.20
37.40	36.5	73.7	121.50	99.45	33.20	62.10	26.20	2.43		2.73	2.45	1.31

APPENDIX: CONTINUED.

No	Sample name	1 PROWID	2 FOURWID	3 NUMWHO	4 RIBDENS	5 LENGTH	6 WIDTH	7 PROHT	8 FOURHT	9 FRSXHT
57.	SCFOSL	54.65	75.20	7.763		31.54	12.11	22.30	59.90	70.63
58.	754F SC	54.50	74.78	8.257		34.74	12.53	21.50	58.00	68.83
59.	756F SC	56.10	75.10	8.038		33.32	12.27	22.70	59.85	69.00
60.	765F SC	48.08	55.81	7.159		21.64	7.94	20.54	53.04	55.93
61.	768F GT	58.40	82.10	8.419		34.76	13.32	25.25	64.50	63.75

* Samples identified as follows: three digit numbers are our field localities; six digit numbers are catalogue designations for samples in the Department of Mollusks, Museum of Comparative Zoology. Suffixial letters as follows: B = *C. blandi*; L = *C. lewisi* (no special letter for *C. regina* samples); F = subfossil sample; SC = South Caicos; NC = North Caicos; MC = "Middle" Caicos; GC = Grand Caicos; EC = East Caicos; NC = North Caicos; WC = West Caicos; LC = Long Cay; SAND = Sand Cay; PR = Providenciales; GT = Grand Turk; PC = Pine Cay; FGC = Fort George Cay; PARC = Parrot Cay; WATC = Water Cay. The following special designations apply: locality 1, 758T, is the second sample (all from one tree) from locality 758; locality

APPENDIX: CONTINUED.

10 UMBWID	11 LIPWID	12 LIPTHK	13 APHT	14 APWID	15 APROT	16 EC	17 FA	18 APTILT	19 WEIGHT	20 HW RATIO	21 PRORAT	22 FOUR-RAT
32.85	27.3	39.2	105.40	86.15	28.40	57.05	26.45	2.21		2.60	2.47	1.26
33.05	35.3	57.6	115.89	93.85	33.35	58.50	26.50	2.27		2.78	2.57	1.29
32.05	29.7	46.8	110.60	87.50	29.65	56.00	27.10	2.09		2.71	2.50	1.26
18.19	14.7	13.2	68.12	54.73	20.73	40.73	19.69	2.09		2.70	2.37	1.06
39.20	25.4	27.0	108.80	87.25	31.15	58.10	28.05	2.13		2.61	2.33	1.27

2, 753A, is the second sample from locality 753; locality 39, REG, is a sample of *C. regina*, area unspecified; localities 56 and 57, SCFOSIS and SCFOSL, are two subfossil samples of *C. regina* from northeastern South Caicos. Units of measurement as follows: 1 and 7 (protoconch width and height) and 11 and 12 (lip width and thickness), in micrometer units, high power, at 18 units = 1 mm; measures 2, 8, 9, 10, 13, 14, 15, 16, 17 in micrometer units, low power, at 8 units = 1 mm; 3 and 4 are counts; 5 and 6 in mm by calipers; 19 in g by Mettler balance; 18, 20, 21, 22 are ratios.